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PRIMITIVE FOSSIL GASTROPODS AND THEIR BEARING ON GASTROPOD CLASSIFICATION

(WITH TWO PLATES)

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INTRODUCTION

GENERAL CONSIDERATIONS

With only one exception that comes readily to mind, the various classifications of the class Gastropoda in current use are the work of neontologists. The living gastropods are classified on the basis of their morphology, largely the anatomy of the soft parts. The fossil forms, or at least the older ones, so far as they belong to genera that are now extinct, are given the scantest of notice and are distributed in an almost haphazard fashion among the families erected primarily for living forms. As neontologists have little familiarity with fossils, unless it be the more recent ones, they are not especially struck by the resulting incongruities. Of course they fail to take the fullest advantage of the information that the older extinct fossil forms can furnish as to the early history of the class and its bearing on phylogeny. Indeed the inaccuracy of such little knowledge as they have of the more ancient fossils is apt to lead them astray.

That the work of the neontologist is nevertheless of the highest importance is too obvious to need comment. He has the entire animal available to him, including the soft parts, and in the main he has made much of his opportunities.

The paleontologist, on his part, suffers from the severe handicap that he can never observe directly the soft parts of the forms that he studies. In a sense he is forced into the role of a mere conchologist. Unfortunately, many paleontologists, inadequately trained in zoology, surrender with resignation, if not with complacency, to what appear to be the necessities of the situation. Nevertheless, it is possible to infer from fossil shells somewhat more of the probable general anatomy of the soft parts than is commonly done and these inferences, if made with due caution, can be useful. Of course they do not stand on the same plane as direct observation; nevertheless to neglect them, or to refuse to give them recognition, however guarded, would be unscientific indeed.

The exception to my original statement that the classification of the Gastropoda is largely the work of neontologists is the work of Wenz, begun in 1938 and unhappily interrupted by his death soon after the close of the second World War (Wenz, 1938-1944). He lived to complete only that part dealing with the prosobranchs. Wenz was a paleontologist with an excellent training. He acquired some familiarity with the older fossil gastropods as a pupil of Prof. Emmanuel Kayser and especially of Prof. Ernst Koken, of Tübingen. His field of specialization since his student days was Cenozoic nonmarine gastropods, a field that did not qualify him particularly for the task he undertook. The novelties introduced by Wenz in 1938 into the classification of the Gastropoda were not in the highest categories but at the familial level. He made a distinct contribution in erecting many families, subfamilies, and superfamilies for extinct genera for which there had long been a need, but the inherent difficulties of working with skeletal material alone and his relative unfamiliarity with the older marine forms made many of his new families mixtures of incongruous elements, and their placement in the higher categories is not always fortunate.

Perhaps the outstanding contribution of Wenz's work in 1938 to the fundamentals of gastropod classification was his suggestion that the isolated, symmetrically paired dorsal muscle scars of *Tryblidium* (Tryblidiacea) might be a very primitive character suggesting the segmentation of the chitons (Wenz, 1938, p. 59). However, in 1938 he allowed himself to be influenced by this idea in constructing his taxonomic hierarchy only to the extent of erecting a separate superfamily, Tryblidiacea, for the genera with symmetrically paired dorsal muscle scars instead of including them with the superficially similar Patellacea, as had been done in effect by previous workers. As is generally recognized, the symmetry in the Patellacea is secondary and superficial, not primitive.

Two years later Wenz proposed a more radically revised classification of the major categories of the Gastropoda (Wenz, 1940). He recognized a major dichotomy within the Gastropoda (excluding the Loricata) between what he regarded as two subclasses, the Amphigastropoda (bilaterally symmetrical, primitively orthoneurous, with a saucer-shaped, conical, or symmetrically spiral shell) and the Prosobranchia (asymmetrical, chiastoneurous, with asymmetrically coiled shell). He elaborates somewhat his invaluable earlier views on the tryblidians but he does not follow the logic of his position and classify them with the chitons. Instead, because of the discovery of multiple paired dorsal muscle scars in the supposed bellerophont *Cyrtonella,* he classifies the bellerophonts with the tryblidians in a subclass, the Amphigastropoda. This action I do not regard as well taken (Knight, 1947b, p. 264, and appendix to this work). Naef, a neontologist, had made a somewhat similar division at an earlier date with the Planospiralia for the bellerophonts (he was unaware of the probable significance of *Tryblidium* and its allies or possibly even of their existence) and the Turbospiralia for the asymmetrical groups (Naef, 1911, p. 159). Naef's Planospiralia, unlike Wenz's Amphigastropoda, was looked on as streptoneurous and, of course, prosobranch.

In the interval between the first draft of the present paper and its completion, an interval required for the preparation of drawings, a significant paper on the aspidobranch Gastropoda and their evolution appeared. This paper, by the distinguished anatomist and physiologist, C. M. Yonge (1947), reports the results of some revealing investigations on the anatomy and functioning of the pallial organs of some aspidobranchs. Yonge does not stop with the recording of observations but proceeds to apply his findings to an interpretation of gastropod evolution just as I have done from a different set of observations. Both Yonge and I have accepted certain findings and interpretations from previous workers and to that extent have a common background. Hence it is not surprising that there is much basically the same in each interpretation. On the whole our acceptance or rejection of the suggestions of previous workers is gratifyingly similar. A minor difference is that he regards Wenz's suggestion that the tryblidians are pretorsional gastropods only as possible (Yonge, 1947, p. 485). With some rearrangements and differences in emphasis from Wenz I accept this as probable. Yonge regards the bellerophonts as prosobranchs, just as I do, and thus rejects Wenz's view that they were "primitively orthoneurous." However, he appears to harbor an unexplained and undocumented idea that although they are symmetrical prosobranchs they had a single dorsal and median retractor muscle (Yonge, 1947, p. 490, fig. 31a). It is my view that the bellerophonts are prosobranch gastropods that have undergone torsion and have retained a high degree of primitive bilateral symmetry including a single symmetrical pair of retractor muscles attached at the distal ends of the columella (Knight, 1947b).

Yonge proposes some phylogenies (Yonge, 1947, p. 490, fig. 31a) toward which I am compelled to be skeptical. I am skeptical of the supposed origin of the Neritacea and the pectinibranchs as branches arising independently and directly from the bellerophonts. The great expansion of the pleurotomarians in the Paleozoic when they overshadowed all other contemporaneous gastropods in diversity of form and number of genera and species provided possibilities that cannot be neglected. For example, the asymmetrical neritaceans and the pectinibranchs may have been derived from asymmetrical ancestors such as some of the numerous and varied pleurotomarians. The pleurotomarians (Pleurotomariacea) include much besides *"Pleurotomaria."* That the present-day *Theodoxus* and the pectinibranchs are not derived from the present-day *"Pleurotomaria"* one can readily concede. It is equally unlikely that the present-day *Haliotis, Scissurella,* the fissurellids, or the patellids are correctly derived from the present-day *"Pleurotomaria,"* as Yonge seems to imply. I am not even prepared to accept *Mikadotrochus beyrichi* (Hilgendorf), the species from which Yonge derives most of his ideas of pleurotomarian anatomy, as properly referred to the genus *Pleurotomaria* Sowerby. That all these may have had common ancestors more advanced than bellerophonts, i. e., advanced to the pleurotomarian stage or farther, seems probable.

The classifications of neontologists are based actually on comparative anatomy, that is to say on morphology, from which they attempt to infer phylogeny, but phylogeny, or descent with change in time, is held very much in the background as an ideal only. The paleontologist alone has spread before him the time sequence, the order in which forms appeared in time. This has been called chronogenesis. Chronogenesis is not a perfect tool, for the fossil record is far from complete and the recognition of phylogenies involves supposed relationships inferred from imperfectly known morphological criteria. Nevertheless, it is a useful tool, if used with caution, and is becoming more and more useful as our knowledge of the life of the past increases.

In summary, all classifications are provisional and hypothetical, based on inferences from more or less complete observations of various phenomena. Certainly any classification based wholly on neontological data or with inadequate attention to or understanding of paleontological data must be almost as defective in the very nature of the case as would be the converse. The present classification is offered as one that at least attempts to give full weight to paleontological data and their bearing on phylogeny. It is admittedly provisional.

PROPOSED CLASSIFICATION

Changes in classification.—The principal novelties of the classification given below consist of the following:

The Polyplacophora are returned to the Gastropoda as one order of a subclass, the Isopleura, proposed by Lankester in 1883. The order Monoplacophora (*Tryblidium* and its allies) is added to the Polyplacophora. I am allowing the Aplacophora to stand close to the Polyplacophora, as do most authors, although without strong conviction. They do not occur as fossils, and paleontology has no light to throw on them. They are probably degenerate, not primitive. These three orders will make up the Isopleura.

In the subclass Anisopleura, also proposed by Lankester in 1883, are included as superorders the Prosobranchia, Opisthobranchia, and Pulmonata, while to the primitive prosobranch superfamilies Bellerophontacea and Pleurotomariacea of the order Archaeogastropoda is added a third, the Macluritacea. Except as affected by the foregoing the remaining more advanced archaeogastropod superfamilies are left untouched as Wenz left them, not because Wenz's treatment is satisfactory but because a complete revision is beyond the scope of this paper. Such a revision is well under way, however, and perhaps in the not too distant future the results may be published.

Phylum Mollusca Cuvier
  Class Gastropoda Cuvier
    Subclass Isopleura Lankester
      Order Monoplacophora Wenz [1]
      Order Polyplacophora Blainville
      Order Aplacophora Jhering
    Subclass Anisopleura Lankester
      Superorder Prosobranchia Milne-Edwards
      Order Archaeogastropoda Thiele
        Superfamily Bellerophontacea Ulrich and Scofield [2]
        Superfamily Pleurotomariacea Wenz [2]
        Superfamily Macluritacea Gill [1]

Other archaeogastropod superfamilies are not considered here, nor are the following orders and superorders:

      Order Mesogastropoda Thiele
      Order Neogastropoda Wenz
    Superorder Opisthobranchia Milne-Edwards
    Superorder Pulmonata Cuvier
  Incertae sedis. *Pelagiella* Matthew, 1895, and allies. Possibly not gastropods.

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[1] Considered in some detail.

[2] Only the earlier, more primitive genera and some living ones considered.

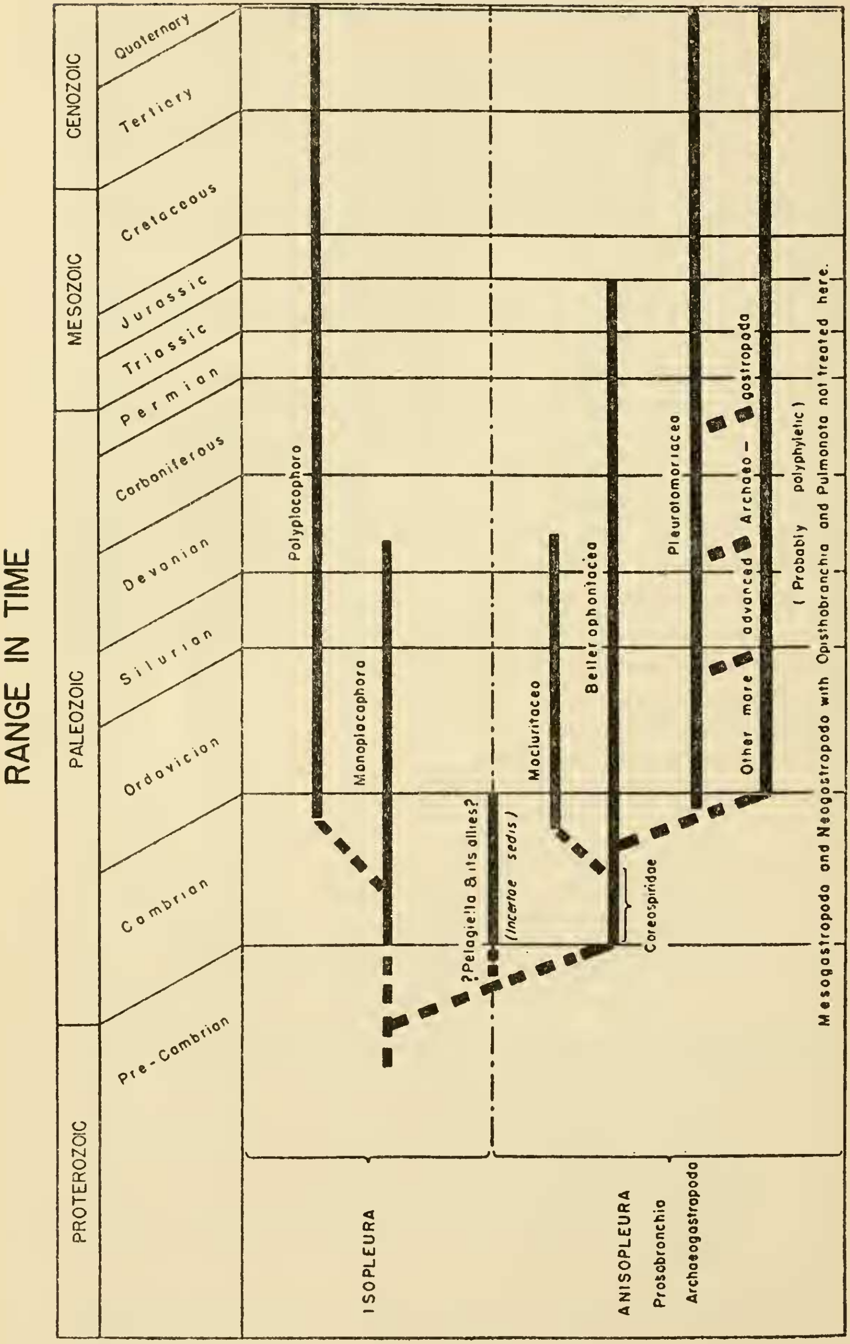

FIGURE 1

(See opposite page for explanation.)

Chronogenesis and range in time.—In order to give an over-all view of the range in time of the two orders of the Isopleura and the three most primitive superfamilies of the anisopleuran prosobranchs, a diagram is presented (fig. 1). It will be noted that the major dichotomy in time (as well as in morphology) is between the Isopleura and Anisopleura in the early Cambrian, at the beginning of the fossil record. It will be noted also that two of the three primitive superfamilies of the prosobranch Archaeogastropoda, the Macluritacea and Bellerophontacea, have been extinct since Devonian and Triassic times, respectively. Only the long-ranging Pleurotomariacea, late Upper Cambrian to Recent, has carried through in several specialized relic families. These give us some clue to the morphology of the soft parts and to the physiology and embryology of the primitive prosobranchs.

EXPLANATORY NOTES

Technical terms.—As far as possible the use of technical terms (other than the formal scientific names of systematic categories) has been avoided. With exceptions to be noted the morphological terms employed are so much in general use by both paleontologists and malacologists that it seems unnecessary to define them.

The term "hyperstrophic" is not a new one but experience suggests that many have only a hazy idea of its meaning. It refers to that

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FIGURE 1.—Range in time of the more primitive categories.

For the benefit of the neontologist interested in geologic time in terms of years and unfamiliar with recent work, the following data are arranged from the Report of the Committee on the Measurement of Geologic Time of the Division of Geology and Geography, National Research Council, for 1949-1950 (p. 18):

Period	Beginning in approximate number of millions of years ago	Approximate length in millions of years
Quaternary	1	1
Tertiary	60	59
Cretaceous	130	70
Jurassic	155	25
Triassic	185	30
Permian	210	25
Carboniferous	265	55
Devonian	320	55
Silurian	360	40
Ordovician	440	80
Cambrian	520	80

Computed probable errors in beginnings: Quaternary ± 50 thousand years, Tertiary ± 1 to 2 million years, Mesozoic ± 5 million years, and Paleozoic ± 10 million years.

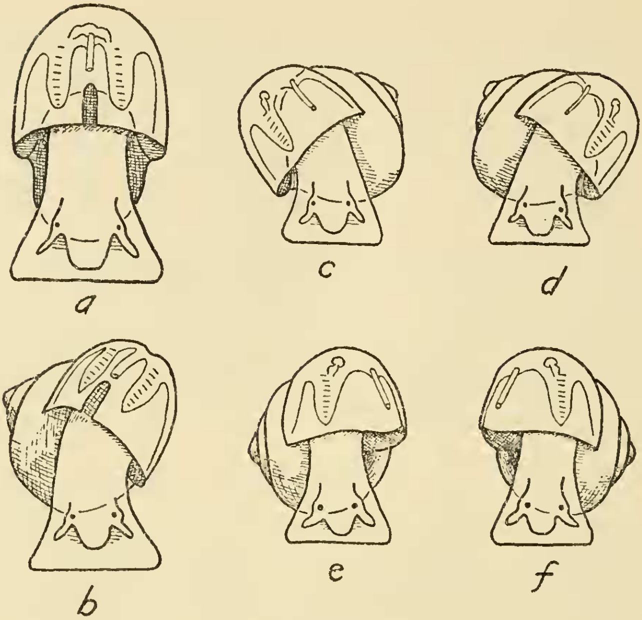

FIGURE 2

a, Isotrophic coiling. Symmetrically coiled in a plane with the sides mirror images of each other. The example is a diagrammatic restoration of a generalized bellerophont. Note the symmetrical and paired ctenidia, the rectum passing through the pericardium and terminating in the anus between the ctenidia and close to the slit, and the symmetrical and paired auricles of the heart.

b-f, Asymmetrical coiling. *b,* Orthostrophic coiling in the pleurotomarians. Although the shell is asymmetrical and orthostrophic the rectum still passes through the pericardium and terminates between the ctenidia close to the slit. Many of the organs such as ctenidia, auricles, etc. are paired. The diagram shows a dextral pleurotomarian. No certainly sinistral ones are known. *c, d,* Orthostrophic coiling at an advanced stage of asymmetry. In the dextral forms the right ctenidium and auricle are lost, the rectum has moved to the right and no longer passes through the pericardium, and the slit has disappeared. *c* shows a sinistral orthostrophic gastropod and *d* a dextral one. Note that the arrangement of the shell and the internal organs in each is the mirror image of the other. A tremendous majority of living gastropods are dextral orthostrophic.

e, f, Hyperstrophic coiling. *e,* sinistral and *f* dextral. Comparing the dextral and sinistral hyperstrophic forms with their orthostrophic counterparts, the relative positions of the corresponding internal organs are the same in each but the direction of asymmetry of the shell is reversed. In the dextral hyperstrophic form the spire protrudes to the left side instead of to the right. The internal organization is dextral, but the shell if oriented in the

[legend continued on opposite page]

sort of coiling in which the shell is inverted and what appears to be the spire is homologous with the base of orthostrophic forms. It is as though the normal spire were pushed through, protruding on the side that is normally the base and the side that normally has the spire resembles a base. The shell resembles superficially a sinistral shell but the soft parts are dextral. A hyperstrophic sinistral shell resembles a dextral one but the soft parts are sinistral.

The term "orthostrophic" is employed for the normal coiling of the great majority of asymmetrical gastropods both dextral and sinistral. The true sinistral gastropod is in all respects a mirror image of a dextral gastropod.

The term "isostrophic" is introduced as an adjective to describe the sort of coiling that is found in many nautiloid and ammonoid cephalopods, and particularly in the bellerophont gastropods. It may be exogastric as in the cephalopods or endogastric as in the gastropods. Isostrophic coiling is symmetrical with the left and right sides mirror images of each other.

Text figure 2 illustrates the different types of coiling described above.

The term "Cambrian" is employed here in the current American sense (Howell et al., 1944, pp. 993-1004) in which beds of Tremadocian age are excluded from the Cambrian. Those are placed as late Lower Ordovician. It is important that the European reader bear this in mind.

Illustrations.—In addition to certain diagrammatic drawings to illustrate various points under discussion I have included drawings of generalized restorations of a number of characteristic Paleozoic genera mentioned in the text. Many of these are yet unfamiliar to any but specialists and it is hoped that the drawings will be of assistance to the general reader in visualizing what must be unfamiliar genera to many. Although these were made from actual specimens of species, they are restorations intended to illustrate generic characters and are not accurate enough to be used for the identification of species.

References.—The list of references will be found on pages 55 to 56. In the text, references to the list are cited in parentheses by author and date. Since I published some years ago descriptions and

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customary way with the spire upward appears to be sinistral. In this paper all illustrated species judged to be hyperstrophic are oriented with the spire downward for this brings the aperture to the same side as in a conventionally oriented orthostrophic shell. See plate 2 on which the Pleurotomariacea shown are dextral orthostrophic and the Macluritacea are dextral hyperstrophic.

figures of the type species of all names of genera based on Paleozoic species published before 1938 (Knight, 1941), no further references to such genera will be given here. References to Paleozoic genera published since 1937 appear in the list. For post-Paleozoic genera the reader is referred to Wenz, 1938-1944, which will suffice for many purposes. If this rather rare work is unavailable, many works on conchology or malacology will do.

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I am indebted to a number of colleagues who have read my manuscript at one stage or another of its development. Among these are Dr. G. Arthur Cooper, Dr. H. A. Rehder, and R. Tucker Abbott, of the U. S. National Museum, and William T. Clench, of Harvard University. Perhaps I am indebted most to Prof. Raymond C. Moore, of the University of Kansas, and to Dr. L. R. Cox, of the British Museum (Natural History). The former has lent encouragement over the five or six years that my ideas have been developing on paper. Both have given the paper critical readings and have furnished the stimulus of dissent from some of the views expressed. I alone am responsible for departures from the orthodox.

ARGUMENT

In order to arrive at hypotheses worthy of attention one must proceed from the known to the unknown, or from the better known to the less well known. Therefore it will be profitable to consider at this point certain selected zoological data, well known, perhaps, to the neontologist but relatively unfamiliar to many paleontologists. Later, paleontological data will be considered.

NEONTOLOGICAL CONSIDERATIONS

MORPHOLOGY OF LIVING POLYPLACOPHORA

The chitons are regarded morphologically as the most conservative in the basic pattern of their organization of all living gastropods, if not of all living mollusks. In respect to certain features, the division of the shell[3] into eight plates and the musculature to operate them, they appear to be highly specialized. Likewise the remarkable shell eyes or aesthetes appear to be developed in some genera, possibly in

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[3] I am regarding the polyplacophoran shell as homologous with the shells of other mollusks. However, it should be noted that at least one recent worker regards it as only analogous (Thiele, 1931, p. 2). Perhaps on further study this very fundamental difference will be resolved.

response, as it were, to the loss of the sense organs of the head.[4] It is these specialized features, the modifications of the primitive basic plan, that distinguish them as chitons. The basic plan of organization is bilaterally symmetrical in all significant respects. There is a flat, creeping foot and well-differentiated head. The head lacks the usual sense organs, possibly due to specialized degeneration. The mouth is anterior and the anus posterior, the digestive tract passes through the pericardium. The gills appear to be true ctenidia and are arranged in pairs in a groove between the shell and the upper surface of the foot on each side of the body, dominantly in the posterior part (Yonge, 1939). The numerous paired ctenidia seem to be metameric repetitions of a primary pair that lie on each side of the anus and just behind the excretory pore (the postrenal gill). The heart is dorsal and posterior. The nervous system is not twisted and shares the bilateral symmetry of the rest of the body. Strictly speaking there is no pallial cavity, but it seems reasonable to regard the posterior and lateral parts of the groove between the shell and the foot that contains the ctenidia and associated organs as strictly homologous with the pallial cavity of more advanced gastropods.

There is no need here to go into a complete morphological description of the chitons. The features to which I wish to draw special attention are the complete bilateral symmetry of all parts and the posterior anus, gills, and heart. It is these features that are regarded as primitive and it is contended that it is the modification of these features in the ancestral stock from which the chitons were derived that gave rise to the Anisopleura, modification primarily through torsion and progressively greater asymmetry.

The chitons appear first in the fossil record in late Cambrian time and are living today. They were never abundant and for most of the time were very rare. They have varied throughout all that vast expanse of time very little indeed.

MORPHOLOGY OF LIVING PLEUROTOMARIANS

The pleurotomarians[5] are classified in the subclass Anisopleura, superorder Prosobranchia, order Archaeogastropoda. They first ap-

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[4] Can it be that the microscopic tubules in the shell of *Tryblidium reticulatum* Lindström described and illustrated by Lindström in 1884 (p. 56) are the tubules of aesthetes instead of some unknown parasitic organism?

[5] The noncommittal vernacular name for this group is employed at this point in its broadest sense, as an informal synonym of Pleurotomariacea. The group has been treated at one time or another as a genus, as a family, or as a superfamily. Wenz in 1938 assigned a little over 200 genera and subgenera, fossil and living, to the Pleurotomariacea.

pear in the fossil record in late Upper Cambrian time.[6] They were the most numerous, varied, and abundant of all gastropods throughout succeeding Paleozoic time. They continue in diminishing numbers and variety through the Mesozoic and carry through to the present as a few genera, in a few families, the most abundant and diversified of which represent two late specializations for rock clinging (Haliotidae, Fissurellidae). Another living family, composed of rare and very tiny forms, is the Scissurellidae. The fourth family of living pleurotomarians, the Pleurotomariidae, is represented in present seas by four rarely seen but large and handsome deep-water species, of great morphological interest because they are seemingly little-changed descendants of early and primitive anisopleuran gastropods. Although entire specimens are very rare, there have been a number of successful dissections with which are associated the names of W. H. Dall, E. L. Bouvier and H. Fischer, and of M. F. Woodward. Dissections have been made also of some of the abundant but specialized Haliotidae, Fissurellidae, and Scissurellidae, but the Pleurotomariidae appear to be less conspicuously specialized for particular environments and therefore more significant for the present purpose.[7]

This is no place to consider the minor anatomical details of the pleurotomarians but certain major features are of importance for our purpose. First, in common with all anisopleurans in which the features are not obscured by later developments, all display the effects of torsion in that the primitively posterior anus and pallial complex

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[6] The genera I refer to, four in number, include three with a deep U-shaped or V-shaped sinus in the outer lip regarded by most paleontologists as homologous to a slit. These are *Sinuopea* Ulrich, 1911 (pl. 2, fig. 1), *Schizopea* Butts, 1926 (pl. 2, fig. 2), and *Dirhachopea* Ulrich and Bridge, 1931. The fourth, *Taeniospira* Ulrich and Bridge, 1931, has a moderately deep pleurotomarian slit and a slit band.

[7] It will be well here to point out that primitive prosobranch gastropods have not a single retractor muscle but a pair of retractor muscles. For example, the living representatives of two of the four existing families of the Pleurotomarianea, the Scissurellidae and the Haliotidae, have a pair of shell or retractor muscles, and a third, the Fissurellidae, has a crescentic muscle accepted as compounded from an original pair. In the Bellerophontacea, supposedly the immediate forerunners of the pleurotomarians, there is likewise a single pair; and in the Neritacea, seemingly an ancient branch from the pleurotomarian stock, and the very primitive Macluritidae there is also a pair. In the living representatives of the Pleurotomariidae alone, of the supposedly primitive stocks, is there a single retractor muscle. This suggests strongly that in this respect these have lost one of the primitive muscles and have advanced far toward *Calliostoma* Swainson, 1840, in the Trochidae, to which they may be more closely related than to the more primitive pleurotomarians.

are found in an anterior position above the head as though they had been twisted into that position. All have a helicoidally coiled, asymmetrical shell at least in late larval stages. But in spite of torsional asymmetry and the beginnings of lateral asymmetry they retain, as a primitive character fully retained in no other group of living anisopleuran gastropods, paired visceral organs, including paired ctenidia, paired auricles of the heart, paired kidneys, etc. The digestive tract passes through the pericardium and the anus discharges between the two paired ctenidia. These are primitive characters and they remind one strongly of the bilaterally symmetrical pairing of the homologous organs in the isopleuran Polyplacophora. They suggest that the Anisopleura were derived ultimately from bilaterally symmetrical, isopleuran ancestors.

Recent and fossil pleurotomarians always, or nearly always, show one distinctive shell feature by which they may be recognized almost at a glance. This is an emargination in the outer lip of the shell. In some of the earliest species it takes the form of a rather deep U-shaped or V-shaped sinus. In others the sinus is V-shaped and it may culminate in a short slit or notch. Still later appear forms with a deep slit and still other modifications, such as a row of tremata, developed independently in several genera, or the apical hole in the shell of the typical fissurellids. In all living pleurotomarians that have been examined the discharge end of the anal tube lies close to the apex of the emargination. Yonge has shown from studies of living examples of *Haliotis* Linné, 1758 (Yonge, 1947, p. 449), of the anatomy of a preserved specimen of *Mikadotrochus beyrichi* (Hilgendorf) (op. cit., p. 454), and of the described anatomy of *Incissura lytteltonensis* Smith (op. cit., pp. 449-458), as well as of living examples of the more highly specialized Fissurellidae, that the respiratory current is created by cilia on the filaments of the ctenidia. The water is drawn into the mantle cavity above and on both sides of the head. It passes backward beneath the ctenidia, impinging on the osphradia enroute, then upward between the ctenidial filaments and outward through the slit or its equivalent. Close to the inner end of the slit (or row of tremata) is the anus at the distal end of the anal tube. The currents, possibly aided by contractions, carry the faeces out through the slit. This is a highly important matter of sanitation for any gastropod with the anus within the mantle cavity and directed anteriorly so as to discharge between a pair of ctenidia. Obviously such a mechanism would not be important for forms with a posterior anus, such as isopleurans, or for those such as the more advanced anisopleurans with an anterior anus but with only one ctenidium on the upstream side, as it were, of the ciliary currents passing through the mantle cavity, or secondarily with a more or less posterior anus as in the opisthobranchs.

ANISOPLEURAN ONTOGENY

There are inherent technical difficulties in the rearing and studying of such extremely small and delicate organisms as the early embryos of primitive gastropods. Because of the complexity of the transformations and the confusing differences in detail from one species to another it is difficult to make generalizations in terms that will be valid in detail for even the few forms for which much is accurately known of the early ontogeny. Furthermore it is difficult to avoid attributing to the embryo adult anatomical features which occur only as rudiments, often as only a few cells not obviously organized, if present at all in the embryo. For example, it is commonly thought that in the process of torsion the gastropod becomes so twisted that the pallial cavity with the pallial complex including anus, ctenidia, kidneys, heart, etc., is translated bodily from a posterior position to an anterior position above the head. In effect this is true but in detail it is not, for in such primitive genera as *Haliotis* and *Patella* Linné, 1758, for example, the "proctodaeum and the solid mesoderm rudiments of the kidneys are the only representatives of the pallial complex when torsion begins. Even in *Viviparus* Montfort, 1810,[8] in which the developmental stages are abbreviated owing to viviparity, the single ctenidium and the visceral part of the pleuro-visceral loop do not develop until . . . after torsion is complete" (Crofts, 1937, pp. 262-263). However, in spite of these difficulties a significant series of events does occur in a definite order.

The early trochophore larva has a dorsal shell gland and a stomodaeum (rudimentary mouth) situated immediately below the ciliated ring of the velum on the ventral side. The shell, secreted by the shell gland, develops from a small disc to a rather deep cup containing the dorsal hump. The proctodaeum (rudimentary anus) is moved ventrally toward the stomodaeum. In the process the rudimentary gut, still without open mouth or anus, is bent into a rough U-shape. This operation is called flexure and is regarded as distinct from torsion for which, however, it lays the foundation. The rudimentary foot appears between the stomodaeum and proctodaeum. The pallial cavity appears as an invagination posterior to the foot. In the meantime the shell

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[8] For *Paludina*, the name employed by Crofts and other embryologists, I am substituting the name *Viviparus*, today regarded as the correct name of the genus concerned.

has continued to grow and, owing to secretion of shell matter more rapidly on the posterior margin, it takes on an exogastric roughly nautiloid form with the primitive apex directed forward.

A highly significant organ, the development of which is completed at the end of the pretorsional stage, is the single "velum retractor muscle" first carefully studied by Crofts in *Haliotis* (Crofts, 1937). The muscle before torsion is asymmetrically placed and slightly spiral in such a way that its retraction rotates the dorsal hump in a counterclockwise direction when viewed dorsally. In passing it will be advantageous to note that the velum retractor persists through life in *Haliotis* as the small left-hand shell muscle and that the hypertrophied right-hand shell muscle, homologous with the single columellar or retractor muscle in most gastropods, is not at this stage represented by a recognizable rudiment of even a single cell. It is probable that the left-hand retractor muscle in the adults of the more primitive aspidobranchs is entirely homologous with that of *Haliotis*. In more advanced types it is lost before maturity.

In *Haliotis* torsion begins at about 30 hours after fertilization of the egg. Crofts (1937, pp. 233-234) reports that the first 90° of torsion takes place in 3 to 6 hours as a result of contraction of the "velvum retractor muscle." The full 180° torsion is not completed until 8 or 10 days later and apparently results from differential growth.

There are curious differences in both the process and time of torsion as reported by different authors for different species and even for the same species. Some of these differences may be caused by the difficulties in observing accurately such small and refractory subjects, but most of them probably reflect actual differences between species. Nevertheless there is general agreement on the fact of 180° torsion at an early embryonic stage.

The torsion results in the pallial cavity's moving from a posterior to an anterior position relative to the foot. Although the organs of the pallial cavity have not yet appeared when torsion begins or are extremely rudimentary they eventually mature after torsion in an anterior position even though their primitive position must have been posterior. Likewise the commissures of the visceral nerve complex mature after torsion as though they had been crossed to a figure 8 during the process, although during torsion they were far too short and rudimentary to be crossed. Torsion, of course, affects relations of the shell to the head and foot so that its apex points to the rear of the head instead of forward.

Before torsion there is some asymmetry in one respect or another, in part no doubt anticipatory in nature and chargeable to acceleration, but after torsion asymmetry develops apace. It is only less marked in those forms that develop primitive paired organs than in those that develop only one member of the primitive pair, usually the definitive left member. The shell is no longer approximately bellerophontiform, but coils in a laterally asymmetrical, helicoid spiral with the spire pointing backward. That in certain groups the shell then becomes symmetrical (*Diodora* Gray, 1821, for example) or that secondary detorsion occurs (opisthobranchs) with a high degree of superficial secondary symmetry is irrelevant to our present discussion. Nor is it relevant that in a few forms the torsion is clockwise resulting in sinistrality (see fig. 3).

To recapitulate, the anisopleuran veliger larva is provided with a dorsal shell gland; the gland secretes a shell that grows by marginal accretion and soon becomes cuplike; concurrently the pallial cavity is invaginated and the body, with the rudimentary alimentary canal, is bent to a U-shape with the procotodaeum within the pallial cavity posterior to the stomodaeum and separated from it only by the rudimentary foot. The U-shaped bending constitutes *flexure*. The next step is *torsion* by which the dorsal hump with the pallial cavity is twisted 180° in a counterclockwise direction (as seen from above) relative to the foot, thus laying the foundation for the prosobranch and streptoneurous conditions. Next comes, as a separate step, the development of lateral asymmetry and the helicoid spire. There are in some advanced stocks still further developments, including detorsion which brings about the opisthobranch condition, euthyneury, and in extreme cases secondary symmetry of a high order.

PRELIMINARY INFERENCES FROM NEONTOLOGICAL CONSIDERATIONS

From anatomy.—It is inconceivable that the living anisopleuran gastropods, which show torsional and generally lateral asymmetry and which are members of the Mollusca, a phylum characterized by basic bilateral symmetry, can be at all primitive in respect to those features. The most ancient anisopleuran group with living representatives, the Pleurotomariacea, appears first in the late Cambrian. Living pleurotomarians show vestiges of bilateral symmetry in the retention of paired visceral organs along with full torsional asymmetry and laterally asymmetrical coiling. The Polyplacophora living today are equally as ancient as the pleurotomarians. They are obviously specialized in respect to the eight-pieced shell, but they retain

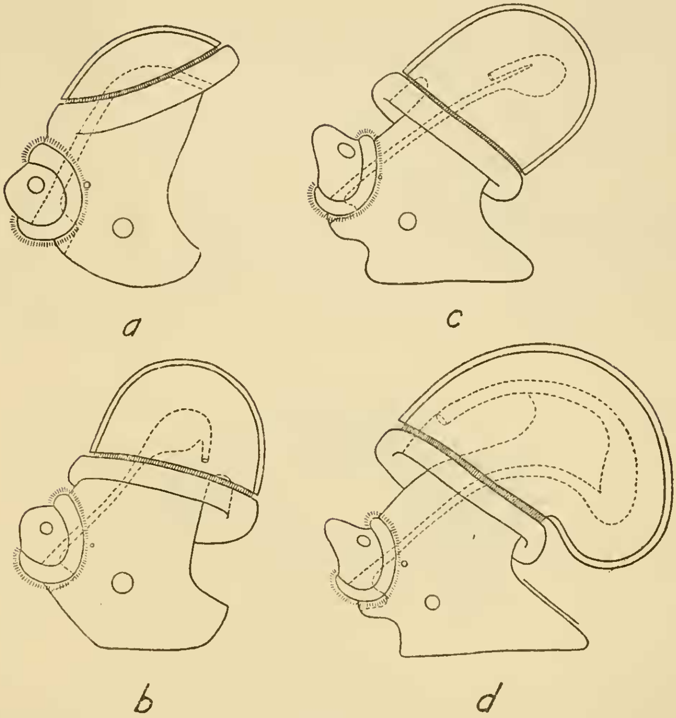

FIGURE 3

Torsion in the embryo of *Viviparus viviparus* (Linné). It should be noted that owing to the viviparity the developmental stages in *Viviparus* are abbreviated. Hence for this reason and because of the highly diagrammatic nature of the drawings (from Naef, 1911, fig. 8, in part) the picture presented is somewhat oversimplified. It is all the more comprehensible for those reasons.

a, Stage where flexure is in progress but torsion not begun. To the left of the figure is the ciliated velum, the cup-shaped shell is above and the rudimentary foot below. The digestive tract is dotted with the mouth below and to the left and the anus high and to the right of the figure.

b, The beginning of torsion. The mantle cavity has appeared and with the anus is turned a little to the right of the animal.

c, Torsion a little more than halfway completed. The anus and mantle cavity are now to the right and a little to the front.

d, Torsion completed. Note that the mantle cavity with the anus is now in front and above the head, it final position. The shell has become bellerophontiform.

strict bilateral symmetry. They cannot be ancestral to the pleurotomarians, but they very plausibly point the way to that more remote ancestor of both chitons and pleurotomarians which must be looked for first in Lower or Middle Cambrian rocks unless it became extinct before Cambrian time with its record irretrievable. Several very distinguished neontologists have speculated as to the probable nature of this common ancestor of both and, indeed, of all the Mollusca. The usual conclusion is that it was a mollusk with a single, low, conical shell, bilaterally symmetrical in all respects, with the anus and pallial complex in the rear, with a differentiated head and a flat creeping foot. In epitome, it would have the basic bilateral symmetry of the Polyplacophora but with a single shell, as in the Anisopleura, but neither coiled nor asymmetrical. Figure 4 shows a reconstruction of such a hypothetical ancestral gastropod, a reconstruction based on pure deduction before anyone had suspected the possibility that supposed Cambrian capulids or patellids that we now recognize as the Monoplacophora had just about the same anatomy. Figure 5 shows a restoration of a generalized monoplacophoran.

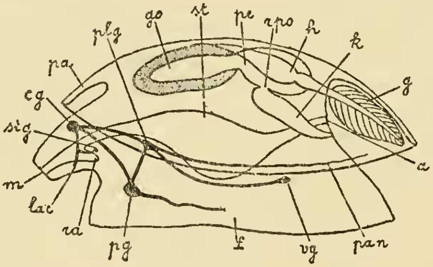

FIGURE 4

Scheme of a hypothetical primitive mollusk viewed from the left side. *a,* anus; *c, g,* cerebral ganglion; *f,* foot; *g,* gill, in the pallial cavity; *go,* gonad; *h,* heart; *k,* kidney; *lac,* labial commissure; *m,* mouth; *pa,* mantle; *pan,* pallial nerve; *pe,* pericardium; *pg,* pedal ganglion; *plg,* pleural ganglion; *ra,* radula; *rpo,* renopericardial orifice; *st,* stomach; *stg,* stomatogastric ganglion; *vg,* visceral ganglion. (After Pelseneer.)

From ontogeny.—Before torsion the cup of the larval shell deepens with flexure of the intestinal tract and because of more rapid growth at the posterior margin takes the form of the beginning of an isostrophic or bellerophonlike coil but with the apex or rudimentary coil forward. It seems reasonable to suppose then that the descendants of our hypothetical ancestral gastropod may have passed through similar stages in the initial process of becoming coiled. Indeed coiling could hardly have occurred in any other way. The development of a higher and higher shell and the initiation of coiling symmetrically in a plane are processes that lend themselves to gradual evolutionary development. If the fossil record is sufficiently complete, we should expect to find among the earliest gastropods forms with complete bilateral symmetry and a low, cup-shaped shell with an apex somewhat in front of the center, others that maintain the bilateral symmetry with a higher, narrower shell and the apex partly coiled forward, and still others with a complete coil, all steps necessary to a gradual evolution. As will be shown in the following parts of this

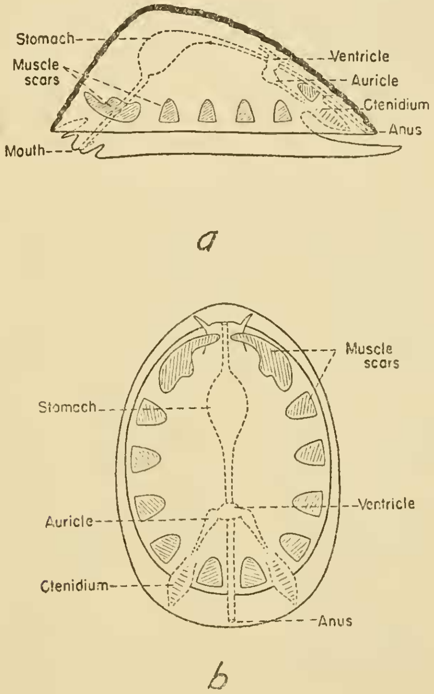

Figure 5

Schematic restoration of a generalized scenellid treated as though it were transparent. In making the restoration there were employed the concepts of untorted bilateral symmetry suggested by the muscle scars of *Archaephiala*. *a*, Left side view; *b*, from above. Except for the muscle scars, note the resemblance to the hypothetical primitive mollusk (fig. 4). The latter was suggested by Pelseneer without reference to scenellids which he regarded as anisopleurans (i .e., *Docoglossa*).

paper, that is precisely what we do seem to find in the earliest fossiliferous rocks.

The next ontogenetic step, the sudden torsional twisting, is spectacular and of the highest significance. Since torsion is not a phenomenon that lends itself to gradual step-by-step development it is highly probable that it occurred just as suddenly phylogenetically as it does today ontogenetically. It is possible, if not probable, that torsion originated as the result of a genetic mutation having its phenotypic expression effective at the veliger stage of the ontogeny (Garstang, 1929, p. 89). This is the view that was set forth by W. Garstang and that has radically altered the thinking of many students of the Gastropoda. If Garstang's view is true, an isopleuran parent may have produced anisopleuran offspring. What could only be regarded as a monstrosity if it had gone no farther was so successful that the strain that carried the genes as a part of its heritage prevailed in competition and eventually brought into being an entire new subclass. (Class in accordance with the usual classification.)

If torsion did arise suddenly in some such manner as Garstang postulated, then the adults of the first torted stock should have resembled their parent in every respect except that they had undergone torsion as larvae. They would have retained all their paired organs symmetrically developed and their shells would have retained their symmetry but with the apex or coil now in a posterior position. They would have retained other peculiarities of the parent stock such as the basic plan of ornamentation. The anus and pallial complex, however, would be above the head and directed forward because of torsion, and since the immediate parent with a posteriorly directed anus and pallial complex had and needed no special provision for clearing the pallial cavity of waste products, the newly torted offspring would be like the parent in this respect. That is to say, it would have no anal emargination in the lip of the shell. In the Early and Middle Cambrian are shells that seem to meet these specifications.

Since the newly acquired orientation results in a position of the anus and pallial complex that would seem to make it difficult to avoid fouling the ctenidia with waste products, we might expect that mutations providing a mechanism for ready disposal of the faeces and urine without fouling would have survival value. Hence it is not surprising to find in Upper Cambrian rocks the first bellerophonts with an anal emargination. It is then present in three bellerophont families. The forms without this sanitary provision disappear shortly thereafter.

The significant embryological studies of neontologists were made on asymmetrical anisopleuran gastropods, the asymmetrical development following closely on torsion. Consequently we should not be surprised to find that lateral asymmetry appeared in the paleontological record soon after the establishment of a line of isostrophic gastropods (bellerophonts) with only torsional asymmetry. This expectation is realized in the appearance of the first known pleurotomarians in late Upper Cambrian rocks.

RECAPITULATION

Summarizing our inferences from neontological data we arrive at the following hypotheses which may be tested against paleontological data. The first is that the Polyplacophora and the pleurotomarians were derived from a common ancestor with complete bilateral symmetry. We infer also that the Polyplacophora have evolved from that common ancestor through the segmentation of the shell but retention of bilateral symmetry. We may further infer that the pleurotomarians have evolved first through the introduction of torsional asymmetry by a single mutation phenotypically effective at the veliger stage of ontogeny (bellerophonts) and later through the initiation of the lateral asymmetry that characterizes all the Anisopleura other than the bellerophonts. (See fig. 6.) Lateral asymmetry is carried progressively much farther in more advanced groups. We may still further infer something of the probable characters of the isopleuran common ancestor of the Polyplacophora and the pleurotomarians and of the intermediate stages between the pleurotomarians and that ancestor.

The immediate predecessor of the pleurotomarians should have had all the characteristics of that group except lateral asymmetry. It should have had torsional asymmetry but lateral symmetry; it should have been coiled tightly or loosely or with a curved apex pointing to the rear in a plane, with each side the mirror image of the other (isostrophic). It should have had an anal emargination when fully established but not when it first suddenly came into being. It, in turn, should have had an immediate predecessor with a high, conical shell with curved apex as the first step toward isostrophic coiling. The high conical shell would of course have been deep and would have so crowded the multiple paired pedal muscles that there would have been room for only a few, perhaps only a single pair. If torsion had taken place the apex of the shell would have pointed backward, if not it would have pointed forward. The last-mentioned stage should have had as a predecessor an untorted mollusk with complete bilateral symmetry and a low, shallow conical shell with little or no flexure of the viscera and, of course, no torsion.

Since, by hypothesis, this most remote stage was ancestral to the Polyplacophora as well as to the Anisopleura it might conceivably display characters basic to the transverse segmentation of the shell into separate plates, characters such as multiple transversely paired pedal or shell muscles. It might have possessed in a rudimentary form traces of the tubules that carry the aesthetes in the tegumentum of modern Polyplacophora.

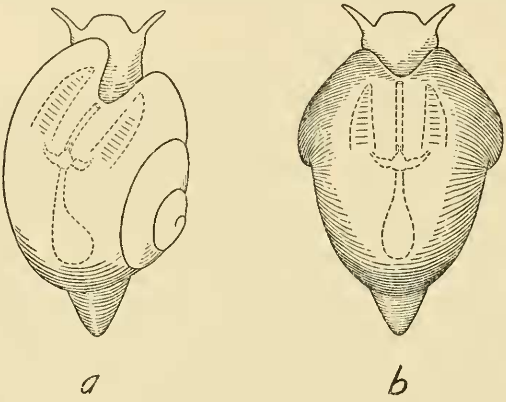

FIGURE 6

a, Schematic drawing of a primitive pleurotomarian seen from above (modified from Naef, 1911). The primitive anal emargination is shown as a U-shaped sinus. The anal tube leading from the stomach is shown as passing through the pericardium and terminating close to the emargination and between a pair of ctenidia.

b, Similar drawing of a primitive sinuitid bellerophont (also modified from Naef, 1911). It is thought to have been very like the primitive pleurotomarians but with complete lateral symmetry. Both have undergone torsion and the pallial complex is anterior instead of posterior.

PALEONTOLOGICAL CONSIDERATIONS

In order to dispel certain misconceptions widely prevalent in neontological circles and, alas, occasionally met with in paleontological circles, a few words in general terms about the gastropods of the Cambrian period may be helpful. These misconceptions arose largely through the efforts of paleontologists of an earlier day to place species, inadequately understood because of poor preservation or some other cause, in established genera, often in order to avoid erecting new genera for them. Since much of the evidence is not explicitly in the literature and cannot be introduced here without making this paper too diffuse, I am forced to speak dogmatically on some points.

There are no Platyceratidae known from rocks older than Middle Ordovician, and no Capulidae in the Paleozoic. That there are both, is a common error. Pleurotomarians do not occur throughout the Cambrian section so far as is known, and only the Late Cambrian bellerophonts are readily recognized as such. There are only four pleurotomarian genera known from Cambrian rocks. (*Pleurotomaria* Sowerby, 1821, is not among them and indeed did not appear in the Paleozoic.) These four are *Sinuopea* Ulrich, 1911 (pl. 2, fig. 1), *Schizopea* Butts, 1926 (pl. 2, fig. 2) (=*Rhachopea* Ulrich and Bridge, 1931, and *Roubidouxia* Butts, 1926), and *Dirhachopea* and *Taeniospira,* both of Ulrich and Bridge, 1931. The anal emargination is a deep, rounded sinus in *Sinuopea* and a deep angular sinus in *Schizopea* and *Dirhachopea,* perhaps culminating in a short notchlike slit in the latter. In *Taeniospira* there is a moderately deep slit and a typical slit band. All four genera are known from beds no older than the latest Cambrian Trempealeauan stage.

Six typical and unquestionable bellerophont genera are now known from the Cambrian and will the neontologist please note that *Bellerophon* Montfort, 1808, is not among them. These are *Owenella* Ulrich and Scofield, 1897, and *Cloudia, Anconochilus, Sinuella* (pl. 1, fig. 10), *Strepsodiscus* (pl. 1, fig. 8), and *Chalarostrepsis* (pl. 1, fig. 12) (all of Knight, 1947 and 1948). The first four have rounded sinuses as anal emarginations, the fifth a deep V-shaped sinus, and the last a deep slit. All these are of late Cambrian age. The earliest is *Strepsodiscus* of the early late Cambrian Dresbachian stage, and three of them, *Strepsodiscus, Sinuella,* and *Anconochilus,* occur earlier than any known pleurotomarian genera. Also there are two isotrophically coiled genera, *Coreospira* Saito, 1936 (pl. 1, fig. 7), and *Cycloholcus* Knight, 1947, both referred to the Coreospiridae. Although neither has an anal emargination, the Coreospiridae are here regarded as primitive bellerophonts. *Coreospira* first appeared close to the boundary between the Lower and Middle Cambrian, probably on the upper side.

There is also still another genus appearing still earlier and ranging throughout the Cambrian that must be considered in this connection. It is *Oelandia* Westergård, 1936, which is here placed in the Coreospiridae. It will be considered more in detail on a later page.

In addition to the bellerophont genera discussed, three genera of macluritoid gastropods occur in the last stage of the Upper Cambrian, the Trempealeauan, *Scaevogyra* Whitfield, 1878 (pl. 2, fig. 7), *Matherella* Walcott, 1912 (pl. 2, fig. 10), and *Kobayashiella* Endo, 1937. All other known Cambrian gastropods are referable to isopleuran monoplacophoran genera. Of these *Helcionella* (pl. 1, fig. 2), and *Scenella* Billings, 1872 (pl. 1, fig. 1), both put in their appearance along with *Oelandia* (pl. 1, fig. 5) in the Lower Cambrian and are thus among the earliest gastropods known. In addition to these there is that very puzzling, problematical group of gastropodlike shells, *Pelagiella* Matthew, 1895, and its allies, that range throughout the Cambrian. These, for reasons given later in this paper, may be regarded as an independent branch from some unknown gastropod ancestor or they may not be gastropods at all.

Although not yet described or announced in the literature chitons (Polyplacophora) are known from Upper Cambrian beds of the Trempealeauan stage.

CLIMBING DOWN THE FAMILY TREE

THE PLEUROTOMARIAN-BELLEROPHONT BRANCH TO THE ISOPLEURAN MONOPLACOPHORA

Continuing to proceed from the better known to the less well known, we will work backward from the living pleurotomarians, from which can be gleaned the basic anatomical details of the group, searching step by step for fossil forms that may be taken for representatives of the various stages in their evolution from their most primitive ancestral stock. The living pleurotomarians are referred currently to the Pleurotomariidae, the Scissurellidae, the Haliotidae, and the Fissurellidae.

In starting on our exploration it seems safe to assume that the basic organization of the most ancient pleurotomarian was essentially the same as that of its living representatives. Such a procedure permits us to drop rapidly down the gastropod family tree or backward in time something over 400,000,000 years to the late Cambrian when the first known pleurotomarians lived, continuing all the while along a branch that is easily recognized because its members show asymmetrical coiling and because of the anal emargination, a slit, sinus, or notch in the outer lip of the shell. From this vantage point in the remote past we may examine our surroundings, particularly those a little more ancient. The objects of our search are forms that resemble the pleurotomarians very closely but are still more primitive.

Contemporaneous with the earliest known pleurotomarians and in part preceding them are the bellerophonts.[9] All but the most primitive are so very similar to the pleurotomarians in a number of significant particulars that on comparative anatomy alone they must be regarded as quite closely related. The shells of the bellerophonts are coiled typically in a close spiral but the coiling is isostrophic rather than helicoidal; the whorl cavity is, of course, very deep and the two symmetrical retractor muscles are inserted one on each side deeply within the aperture at the two ends of the columella in such a position that their retraction would withdraw the head and foot within the aperture; there is an anal emargination, a U-shaped or V-shaped sinus or a slit, just as in the contemporary pleurotomarians. In fact the only obvious particular in which the bellerophonts differ from pleurotomarians is that the coiling is isostrophic and the shell is a symmetrical spiral. Clearly then, the bellerophont, like the pleurotomarian, was a prosobranch, but a symmetrical prosobranch. Since lateral symmetry is a primitive character in the mollusks this is precisely what one might expect in the immediate ancestor of the pleurotomarians which themselves retain more or less symmetrically paired organs. It is commonly believed by neontologists that asymmetry is an immediate and necessary result of torsion. No doubt the belief is well founded in the sense that torsion precedes asymmetry and is a prerequisite for it, but if the bellerophonts are prosobranchs as their morphology strongly suggests and if torsion is the factor that distinguishes a bellerophont from an immediate laterally symmetrical isopleuran ancestor, then, as the time factor insists, it is not necessary to suppose that asymmetry was an immediate consequence. Of course torsion furnished the unstable condition that ultimately led to asymmetry.

Again surveying our surroundings, this time from the apparent base of the bellerophont stem, we meet with two more genera that have the characters one would expect of the very primitive bellerophonts. One is *Cycloholcus* from the base of the Upper Cambrian Dresbachian stage and the other is *Coreospira* (pl. 1, fig. 7) (both referred to previously) from close to the boundary of the Middle and the Lower Cambrian, probably on the upper side of the boundary. Both of these forms are isostrophically coiled and thus in this respect are in accord

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[9] Some views expressed by Thiele, 1935 (p. 1125), and Wenz, 1938 (pp. 58-60), on the probable anatomy and physiology of the bellerophonts will not, I think, bear close scrutiny. Since I do not wish to interrupt the present argument to give the reasons for my contrary views that the bellerophonts are prosobranchs instead of primitively orthoneurous "Amphigastropoda," as Thiele and Wenz supposed, I am discussing the matter in an appendix to this paper.

with the bellerophonts. Unlike previously recognized bellerophonts there is no emargination in the lip that corresponds to the anterior lip. This appears puzzling unless we remember that there is a feature we were to look for in the primitive bellerophont.

Further exploration turns up the genus *Oelandia* (pl. 1, fig. 5), a genus that may be interpreted most plausibly as being closely related to *Cycloholcus* and especially *Coreospira* (pl. 1, fig. 7). *Oelandia* has been associated commonly with *Helcionella* Grabau and Shimer, 1909 (pl. 1, fig. 2). For example, Wenz in 1938 (p. 88) places it in the subfamily Helcionellinae in the family Tryblidiidae. There is indeed a resemblance—a resemblance that appears to me to be honestly come by but still not decisive taxonomically. In *Helcionella* the apertural margins are in a flat or nearly flat plane. In *Oelandia* however the margins tend to be curved and one end, the end toward which the apex bends, is considerably extended and often tilted up as though to form a trainlike hood. If one attempts to think in terms of soft anatomy this hood seems anomalous over the head but fits nicely as a hood over the posterior train of the foot. Hence the extended or up-tilted end is here regarded as posterior. If this hypothesis is accepted the apex is posterior and *Oelandia* may be considered to be a very primitive isostrophic prosobranch gastropod in the Coreospiridae, one that has not yet advanced to the stage of close coiling. Of course the anal emargination has not yet appeared. *Helcionella* remains in the Isopleura with the nontorted Monoplacophora. *Oelandia* is an anisopleuran that may have been derived directly from *Helcionella* and retains its characteristic ornamentation. Torsion may have first taken place between these two genera in earliest Cambrian or in pre-Cambrian time. This possibility will be discussed again.

The Coreospiridae are bellerophonts in respect to the shell coiled or nearly coiled with lateral symmetry in a plane. In some other respects they resemble more closely the group that we next meet with, for although we have reached in *Oelandia* (pl. 1, fig. 5) close to the beginning of the fossil record we have not fully surveyed its contemporaries. There are still three kinds of gastropods or supposed gastropods represented with *Oelandia* in the Lower Cambrian rocks. One of these three, *Pelagiella* and its allies, seems anomalous from any viewpoint and will be reserved for later discussion. The other two fit into our picture very nicely. Both are cup-shaped and show complete bilateral symmetry. Their ornamentation consists of transverse undulations somewhat similar to those of *Coreospira* (pl. 1, fig. 7) and *Oelandia*. One, the genus *Scenella* Billings, 1872 (pl. 1, fig. 1), is cup-shaped with a conical shell and the apex tipped toward the narrower end. The shell of the other genus, *Helcionella* (pl. 1, fig. 2), is also cup-shaped, and includes species that are low and broad as well as others that are high and narrow. In both the apex points toward the narrower end of the aperture and in the high and narrow species it is almost hooked. None of these have the hoodlike train of *Coreospira, Oelandia,* and narrow bellerophonts in general.

Although we know nothing of the internal organization of either *Helcionella* (pl. 1, fig. 2) or *Scenella* (pl. 1, fig. 1) by direct observation, their external features such as shape and ornamentation suggest rather strongly that they belong to a family that continues into the Devonian. Specimens of an Ordovician genus of this family, *Archaeophiala*[10] Perner (pl. 1, fig. 3), preserve the muscle scars beautifully. The scars are strongly pigmented and for that reason are unusually sharp and clear. (See Knight, 1941, pl. 3, figs. 3a-b.) These scars are 12 in number and are arranged in a ring deep within the margin of the shell. Two of the scars are larger than the others and are made up of three parts. These tripartite scars, which occur at one end, may be regarded as compound and perhaps as representing the scars of three muscles each. The other 10 scars are simple and probably are the scars of single muscles. These 12 (or 16) scars are in bilaterally symmetrical pairs. The pair of large compound scars lies at the end toward which the apex lies and very nearly closes the circle at that end. The scars of the other five pairs follow symmetrically on either side until the circle is nearly closed at the other end. There is a line of much fainter, unpigmented scars outside of the principle ring. The six (or eight) pairs of pigmented scars were probably points of attachment for symmetrically paired muscles connecting the shell to the foot. One can hardly guess what function was served by the muscles that made the more obscure scars outside those of the main circle but these shadow scars appear to be characteristic of the group.

Two exceedingly important inferences are suggested by the scars of *Archaeophiala* (pl. 1, fig. 3). The first inference is that the soft anatomy was bilaterally symmetrical throughout, that is to say the animal had not undergone torsion. This is an inference primarily from the complete bilateral symmetry of the paired muscle scars,

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[10] I am employing *Archaeophiala* rather than *Tryblidium* to typify the gastropods with paired muscle scars for the reason that its shape, which is essentially that of *Scenella* and the lower, cup-shaped *Helcionella,* suggests that it is the more primitive. Although their muscle scars are virtually identical, I am placing each in a separate family, as will be seen, since each seems to be a member of a different series, each with its characteristic shape.

supported by the lack of an area between scars at either end for a pallial cavity. The second inference is that the end that has the large compound muscle scars and toward which the apex lies is anterior. This follows as probable from a corollary to the principal of cephalization to the effect that "heteronomous segmentation is an expression of cephalization." If one takes these two inferences together with the previous inference that such Cambrian genera as *Scenella* (pl. 1, fig. 1) and at least the lower, cup-shaped species of *Helcionella* (pl. 1, fig. 2) are organized in a similar way we have a working hypothesis as to the organization of these very important early forms. It seems quite certain that the superficial resemblances of these Cambrian cup-shaped forms to the living prosobranch patellaceans or capulids or to the equally prosobranch Paleozoic platyceratids is as surely a matter of convergence as is the equally superficial resemblance of all of them to the pulmonate ancylids.

It seems probable that a prerequisite for torsion was a reduction in the hypothetical six or eight paired shell muscles to a single pair. What better mechanism to give mutations accomplishing such a reduction survival value could have been devised than the development of high, narrow shells, such as actually occurred in some Lower and Middle Cambrian species currently referred to *Helcionella* (pl. 1, fig. 4). In these the hypothetical six or eight pairs of muscles, if present, would be crowded together. Perhaps, owing to this crowding, mutations that would effect the reduction of the six or eight pairs to a single pair through the elimination of all but one of the pairs would have survival value. If the suggested reduction actually took place the foundation was laid for torsion. All that would be required further is that through a genotypically small mutation the rudiments of one muscle of the pair (the left one) should develop in the early veliger larva earlier than those of the other. As has been shown by Crofts (1937), the retraction of such a single asymmetrical "velum retractor muscle" in the early veliger is what actually initiates torsion in *Haliotis*. Undoubtedly when torsion first appeared in the remote ancestors of *Haliotis* the same mechanism was responsible for it.

Both *Helcionella* (pl. 1, figs. 2 and 4) and *Scenella* (pl. 1, fig. 1) appear in Lower Cambrian rocks. It seems probable that *Helcionella* and *Scenella* had a common ancestor in early Cambrian or in pre-Cambrian time. *Chuaria* Walcott, from pre-Cambrian rocks of the Grand Canyon region, has been suggested as the most primitive ancestral gastropod but the only known specimens of the only known "species," all of which I have examined, are so very poorly preserved that it is utterly impossible for me to recognize them as gastropods or anything else. The most I can say of the specimens is that they may be organic in origin.

In descending the family tree we have passed from the earliest forms that can be assigned to the Anisopleura with assurance, the bellerophont cyrtolitids and sinuitids, such as *Strepsodiscus* (pl. 1, fig. 8) and *Sinuella* (pl. 1, fig. 10) of the lower and middle Upper Cambrian, through the probably anisopleuran Coreospiridae, to the isopleuran *Helcionella* (pl. 1, fig. 2) and *Scenella* (pl. 1, fig. 1) of the Lower and Middle Cambrian. In doing so we have passed along two exclusively Cambrian limbs, the Coreospiridae and the Helcionellidae. The Coreospiridae resemble the bellerophonts externally except that there is no feature that can be assigned the function of the bellerophont anal emargination. The Helcionellidae resemble the Coreospiridae except that the direction toward which the apex bends is interpreted as anterior. As stated above, there are with the genus *Helcionella* (pl. 1, figs. 2 and 4), as currently understood, species that have a high shell with a strongly curved apex and others, more similar to the type species, with a low shell with the apex so short and blunt that in some specimens it is almost an overstatement to say that it is curved at all. These appear to make a continuous series. Our hypothesis requires that torsion was initiated somewhere between the untorted helcionellids and torted bellerophonts. The evidence for one point in the chain as against another is not very compelling. I have placed the dividing line between *Helcionella* (pl. 1, fig. 2) and *Oelandia* (pl. 1, fig. 5), placing the former in the Isopleura with the Monoplacophora and the latter in the Anisopleura with the bellerophonts. If anyone prefers to class the Coreospiridae with the Monoplacophora or *Helcionella* with the bellerophonts, I cannot quarrel too vigorously with the preference. There is insufficient evidence. As the muscle scars, which might give more objective evidence, are unknown in *Helcionella* and in both *Oelandia* (pl. 1, fig. 6) and *Coreospira* (pl. 1, fig. 7) we are left with little but interpretations from weak morphological data as basis for a decision, however tentative. What little objective evidence there is lies in the similarity of the ornamentation in the Helcionellidae and the Coreospiridae and in differences in the apertural margins. This suggests that both of them are allied to each other and to the Scenellidae where the ornamentation follows a similar pattern, but that for some reason, assumed to be torsion, the apertural margins are different. At whatever point torsion was introduced, our hypothesis requires that it was in the more or less advanced descendants of *Scenella* and *Helcionella* that conceivably retained a similar type of ornamentation.

Just as the neontologists have employed restorations of the hypothetical primitive mollusk with fruitful results, so the paleontologist with even more actual data, the fossil shells, may employ them also. Not only does the paleontologist have fossil shells that tend to support the scientific speculations of the neontologist but he has others to which he may attempt to fit the soft parts of a generalized gastropod and form judgments from the plausibility of the results as to what the animal as a whole may have been like. Some of these hypothetically restored gastropods tend to fill gaps between the untorted

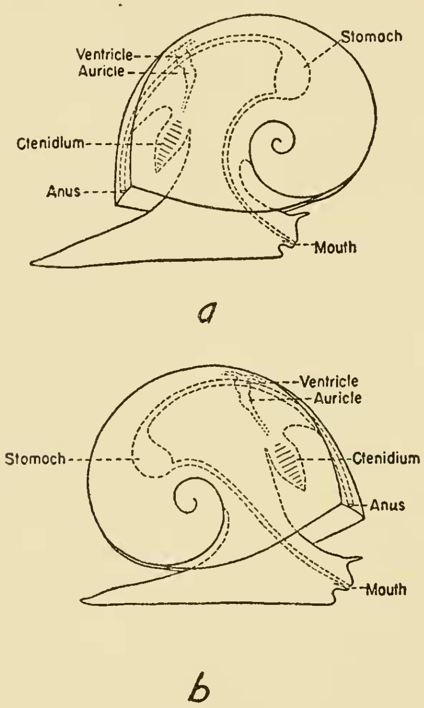

FIGURE 7

a, Schematic restoration of *Coreospira* as a monoplacophoran isopleuran.
b, Schematic restoration of *Corcospira* as an isostrophic anisopleuran, a bellerophont without an anal emargination. The latter seems a much more plausible restoration than the former. Of course, neither restoration may approximate the truth, but in that case *Coreospira* would probably not have been a gastropod. It is understood that such organs as ctenidia, auricles, etc., are paired in both restorations. The probable retractor muscles are not shown.

monoplacophoran and the torted bellerophont which in turn connects closely with the pleurotomarians.

For example, text figure 7 shows two restorations based on the known shells of *Coreospira* (pl. 1, fig. 7). Figure 7, *a,* shows the shell and hypothetical soft parts restored as an isopleuran monoplacophoran. Figure 7, *b,* shows the same restored as an anisopleuran bellerophont. Obviously the second yields a plausible picture of the probable relationship of shell and soft parts. It looks comfortable. The monoplacophoran restoration is too fantastic for even tentative acceptance. Even though one should restore the soft parts to display more primitive isopleuran features, a row of muscles, a very shallow posterior pallial cavity, etc., we still would have the coiled shell suspended above the head in a most unacceptable fashion, as well as a narrow, coiled visceral mass entirely incongruous on a monoplacophoran. Surely it is difficult to accept *Coreospira* as other than a primitive bellerophont.

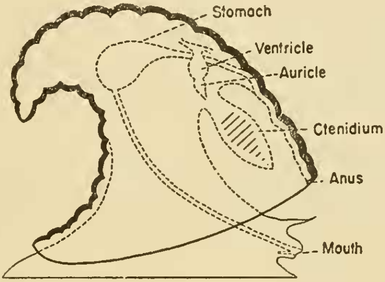

FIGURE 8

Oelandia restored as a bellerophont even more primitive than *Coreospira.* It presents a harmonious and plausible picture. A restoration as a monoplacophoran is quite as unacceptable as is the same restoration of *Coreospira.* As I have pointed out previously the trainlike hood over the posterior part of the foot is a critical feature—a feature that is shared with several bellerophont genera with narrow shells.

Figure 8 shows a restoration of *Oelandia* (pl. 1, fig. 5), believed to be a bellerophont even closer to the Monoplacophora than *Coreospira* (pl. 1, fig. 7).

THE POLYPLACOPHORAN BRANCH

The procedure of working backward may be likened to selecting one terminal twig of a tree from among very many, a twig on a branch that by preliminary inspection took its origin far down on the trunk, and then following that branch still farther down until one is led by the process to what appear to be the roots. But our metaphorical tree, from preliminary inspection in very poor light (for let us assume that we are feeling our way in the dark of the moon), seems to have more than one main branch. One of these which we will call the Polyplacophora, appears near the roots to lie close to the branch that we have been tracing backward with apparent success. Let us examine it further.

The chitons or Polyplacophora, far from abundant today, have always been rare in the fossil record. Nevertheless they are reported in the literature as distributed throughout geological time from rocks as early as Lower Ordovician and in the collections of the United States Geological Survey housed in the United States National Museum are specimens of unquestionable polyplacophoran plates from the late Upper Cambrian Eminence dolomite of Missouri. These specimens, belonging to species and perhaps genera yet undescribed, are nevertheless typically polyplacophoran in every detail including the peculiar surface sculpture, common to all chitons, possibly to be associated with the remarkable shell eyes, or aesthetes, developed in this group.

Thus our leap backward in time along the polyplacophoran limb of our metaphorical tree carries us almost exactly as far as our leap along the pleurotomarian limb, to latest Cambrian time. However, we find no obvious intermediate connections with any monoplacophoran. Our only clue appears to be offered by the paired multiple dorsal muscle scars of *Archaeophiala* (pl. 1, fig. 3) attributable by analogy to *Helcionella* (pl. 1, fig. 2) and *Scenella* (pl. 1, fig. 1), possibly reinforced by what appear to be tubules in *Tryblidium* very similar to those which carry the nerves for the aesthetes in chitons. In *Archaeophiala* (and in *Tryblidium*) the number of pairs is six[11] but the pair of large scars at the end regarded as anterior are compound and made up of three smaller elements so that the basic number of pairs might be regarded as eight. One might infer that the eight-segmented shell of the polyplacophoran was merely the single shell of the monoplacophoran separated into eight segments to correspond with the eight pairs of shell muscles.

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[11] It may be significant that the embryos of living polyplacophorans first develop six shell plates. The other two, the terminal plates, are added at a later stage (Garstang, 1929, p. 78).

RECLIMBING THE TREE

For recapitulation it may be well to reverse our course and summarize our results by ascending the pleurotomarian branch of the family tree beginning with the Monoplacophora. We will still hold to this one line, lest we go entirely astray, and we will arrive at the present-day level along a limb with nothing more advanced than the highly specialized relics of the once great pleurotomarian stock.

Throughout rocks of Cambrian age we find what appear to be primitive gastropods with low, cuplike shells. The apex is subcentral or anterior and there is no posterior train. All have rather coarse transverse plicae or costae and finer ornamentation as well. They are believed to have six (or eight?) symmetrical pairs of adductor muscles and not to have undergone torsion. Typical of these early Cambrian genera are *Scenella* (pl. 1, fig. 1) and those species of *Helcionella* (pl. 1, fig. 2) that have the low cuplike form of the genotype. Probably these or similar forms were in existence in late pre-Cambrian time.

Concurrent with the more typical species of *Helcionella* (pl. 1, fig. 2) are other species, that should probably be referred to another as yet unnamed genus, which have very high, narrow shells (pl. 1, fig. 4). It is possible that in these forms the adductor muscles were so crowded that their number was reduced to a single pair, seemingly a prerequisite for the initiation of torsion. Likewise in the early two-thirds of Cambrian time are found species of *Oelandia* (pl. 1, fig. 6), much like *Helcionella* externally but with an extended or up-tilted margin under the apex that has the same shape as the posterior train found in narrow bellerophonts. Accepting it as homologous, we then must accept *Oelandia* (pl. 1, fig. 5) as having undergone torsion but in most other respects to have retained at least some of the external features of *Helcionella*. It is possible that it was the first bellerophont and first prosobranch. Its apex is posterior but still not truly coiled. However, close coiling is found in *Coreospira* (pl. 1, fig. 7) partly contemporaneous with all these but appearing first a little later and still without the anal emargination.

In late Cambrian time we find a number of bellerophonts each provided with an anal emargination: *Strepsodiscus* (pl. 1, fig. 8) and *Cloudia* in the Cyrtolitidae; *Sinuella* (pl. 1, fig. 10), *Owenella*, and *Anconochilus* in the Sinuitidae; and *Chalarostrepsis* (pl. 1, fig. 12) in the Bellerophontidae. With this beginning the bellerophonts deploy throughout Paleozoic time and have their last representatives in the Triassic.

In the latest Cambrian the first pleurotomarians put in their appearance, mostly primitive pleurotomarians with either rounded or angular sinuses, *Sinuopea* (pl. 2, fig. 1), *Schizopea* (pl. 2, fig. 2), and *Dirhachopea.* The anal emargination in *Taeniospira* is a true slit. The anal emargination became a true slit in Early Ordovician time in a number of genera, some as yet undescribed. During the remainder of the Paleozoic the pleurotomarians proliferate greatly and seemingly gave direct rise independently to a number of nonpleurotomarian aspidobranch stocks and through these to most if not all of the more advanced gastropods. They continue in declining numbers through the Mesozoic and Cenozoic and survive today in greatly reduced numbers as relic families adapted to special environments.

In late Cambrian rocks in beds almost contemporaneous with those containing the earliest known pleurotomarians, the first known polyplacophorans appear, typical chitons in all respects. These also continue to the present day but always as relatively few forms mostly adapted to rock clinging. They, like the anisopleuran branch, seem to have been derived from primitive, untorted monoplacophorans but through an entirely different set of modifications. The primitive isopleuran condition continued, for in the polyplacophorans there was no torsion, but the primitive single cuplike shell is replaced by eight transverse plates. Perhaps these eight plates represent the primitive shell which may have become divided transversely in accordance with the possibly eight pairs of shell muscles.

EXPLORATION OF OTHER EARLY BRANCHES

In our climb down two branches of the gastropod family tree, arriving along both at the same main stem, we have followed what appears to be a logical and straight course, paying no attention to other nearby branches. But there are other nearby branches not too far above the roots and it would be improper to leave them out of consideration altogether, especially as the light is very poor.

THE PATELLACEA

First there is the branch that we will call the Patellacea. It is well represented in our living faunas and goes far back into geological time. The patellaceans include simple, cuplike shells that show externally full bilateral symmetry and resemble very closely those that we are here regarding as monoplacophoran isopleurans. However, the anatomy and ontogeny of living representatives show unequivocably that the symmetry of the shell is superficial and secondarily derived. They are classified by neontologists as Archaeogastropoda in the Prosobranchia. Although primitive in many respects, they show in their soft parts and in their ontogeny both torsional and lateral asymmetry. Can it be that in following our branch backward in time we have become confused in the darkness and, instead of passing from the earliest bellerophonts to monoplacophorans, we have stepped across onto another superficially very similar but different branch? Can it be then that what we are calling monoplacophoran isopleurans are in truth nothing more than very ancient patellaceans? Except for Wenz, most previous authors have so regarded them. However, I think not, for there are characters in both groups, very obscure ones to be sure, that seem to indicate the contrary.

The significant clues have to do with the scars of the shell muscles in each group. In the patellaceans the muscle scars form a continuous horseshoelike crescent, open anteriorly, for the shell muscle does not intrude upon the region occupied by the anterior pallial cavity. The shell muscle is composed of closely applied bundles of muscle fibers and in some species this is reflected in the scar by knots, so to speak, in the continuous scar that suggest the discrete scars of the typical monoplacophorans. But these knots in the patellacean scar are not symmetrically paired while the discrete scars of the monoplacophorans are. They reflect the basic asymmetry of the patellaceans. Likewise the anterior opening of the patellacean scar seems to reflect the torsion of the primitively posterior pallial complex and cavity to an anterior position above the head. Although there is in the patellaceans a very thin scarlike line connecting the open ends of the horseshoe, it is apparently not the scar of the pedal muscle but merely the line of attachment of the mantle to the shell, analogous to the pallial line of the pelecypods. The monoplacophorans are here conceived to have included also forms with a continuous muscle scar, such as *Archinacella* Ulrich and Scofield, 1897, as well as those with discrete paired scars, but in both types the scars have elements that close or nearly close the circlet anteriorly and these elements seem to be continuations of the scars themselves. This suggests that these forms, like the Polyplacophora, do not have an anterior pallial cavity and supports our inference that the Monoplacophora have not undergone torsion. That the scars are narrower anteriorly may be accounted for if we imagine that the muscles attached at this part are extensions from the pedal muscles at each side arching over the head.

Although Wenz did not recognize them as such, it is my opinion that the late Paleozoic genera, *Metoptoma* Phillips, 1836, and *Lepetopsis* Whitfield, 1882, are not monoplacophorans but are referable to the Patellacea. Both have continuous, horseshoe-shaped muscle scars, completely open at the anterior end. I would also assign *Palaeoscurria* Perner, 1903, to the Patellacea. Perner described and figured for this genus an open horseshoe of almost discrete muscle scars but I have examined the types of his genotype species and can find no objective evidence for the existence of such a feature (Knight, 1941, p. 231). Nevertheless, there is no direct evidence for any other sort of scar, possibly because the matrix is too coarse to record such delicate features. However, the shape of the shell is so similar to that of *Lepetopsis* that I shall provisionally associate the two. The fossil record of the Patellacea is then continuous from at least Mississippian and perhaps from Silurian time to the present. I know of no Patellacea from rocks earlier than Silurian, nor do I know any forms transitional from pleurotomarian to patellacean unless the very imperfectly known *Halophiala* Koken, 1925, from Ordovician rocks may be so regarded.

MACLURITES AND ITS ALLIES

Beginning in the early Trempealeauan stage of the Upper Cambrian and ranging into the Middle Devonian are a series of genera that give the appearance, at least, of being coiled sinistrally. These genera are here united taxonomically not only by the apparent sinistral coiling, but by another feature as well. This feature, a difficult one to describe, consists in most of these genera of a peculiarity of the region surrounding the umbilicus or that part of the shell usually called the base whereby the "basal" part of the whorl profile is rather sharply arched, most conspicuously so where there is an open umbilicus. This sharp arching of the supposed basal part of the whorl resembles a notch keel with an internal channel. In many forms it is clearly the locus of a sinus in the lip. The following 17 genera, most of them commonly regarded as sinistral, make up the group I have in mind:

From the Upper Cambrian rocks

Kobayashiella Endo, 1937.
Matherella Walcott, 1912 (pl. 2, fig. 10).
Scaevogyra Whitfield, 1878 (pl. 2, fig. 7).

From Ordovician rocks

Antispira Perner, 1903.
Barnesella Bridge and Cloud, 1947 (p. 545).
Clisospira Billings, 1865.
Helicotis Koken, 1925.

Laeogyra Perner, 1903.
Lecanospira Ulrich, in Butts, 1926 (pl. 2, fig. 8).
Lesueurilla Koken, 1898.
Maclurites LeSueur, 1818 (pl. 2, fig. 12) (=*Maclurina* Ulrich and Scofield, 1897).
Macluritella Kirk, 1927.
Matherellina Kobayashi, (1933) 1937.
Mimospira Koken, 1925.
Palliseria Wilson, 1924 (pl. 2, fig. 11) (=*Mitrospira* Kirk, 1930).
Versispira Perner, 1903.

From Silurian rocks

Onychochilus Lindström, 1884 (pl. 2, fig. 9) (=*Palaeopupa* Foerste, 1893).

From Devonian rocks

Sinistracirsa Cossman, 1908 (=*Donaldia* Perner, 1903, preoccupied, and *Boycottia* Tomlin, 1931).
Omphalocirrus Ryckholt, 1860 (=*Coelocentrus* Zittel, 1882, *Polyenaulus* Ethridge, 1917, and *Arctomphalus* Tolmachoff, 1926).

Thus I have grouped together (with one or two superficially dextral genera) all the Paleozoic genera commonly regarded as sinistral except *Antitrochus* Whidborne, 1891, which I refer tentatively to the Trochonematacea, *Agnesia* Koninck, 1883, and *Hesperiella* Holzapfel, 1889, both pleurotomarians and possibly congruent, and *Cambodgia* Mansuy, 1914, a pseudomellaniid. Other typically dextral genera are known to have a few sinistral species, as well.

Up to this point I have spoken of the gastropods of the group we are considering as "apparently" sinistral, that is to say, when the shell is oriented in the arbitrarily conventional position [12] with the spire upward (or the umbilicus downward), the aperture is below and to the left rather than to the right as in the vast majority of gastropods. In the truly sinistral gastropod all organs of the body are reversed in position from that of the dextral gastropod beginning ontogenetically with the early cleavages of the egg. The reversal appears to be the result of a mutation that may occur in some individuals of normally dextral species, or that has become fixed in the heritage of some species in genera that are otherwise dextral, or of a few entire families.

Sinistrality is well known among living gastropods but relatively it is very rare. Likewise it is known among fossil Gastropoda. Of

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[12] I employ the illogical conventional orientation preferred by English, German, and American authors.

the genera dealt with above *Antitrochus* and *Cambodgia* are probably sinistral. The pleurotomarians *Agnesia* and *Hesperiella* present a still different picture that I hope to discuss at another time. But in all cases sinistrality is a deviation from the basic plan and seemingly occurs only as the result of mutations that may or may not become fixed in the heritage of a group. It occurs sporadically in various only remotely related groups and is probably of no selective value, positive or negative, to its possessor. The rarity of sinistral gastropods is related to the primitive torsion and asymmetry of the Anisopleura. Presumably it was of such a nature as to produce dextral forms, and deviations from the plan require a relatively rare mutation in which all parts of the organism at all stages were reversed. Therefore the occurrence of a relatively large number of apparently sinistral forms classifiable into a relatively large number of genera very early in the history of the class is startling and affords grounds for suspicion that these forms are not truly sinistral.

Among living gastropods there is another phenomenon very much rarer than sinistrality which gives rise to a shell that has the appearance of being sinistral but the organs of the anatomy are not reversed from the position in dextral Gastropoda. The entire animal, including both soft parts and shell, is actually dextral in this case, and the shell is ultradextral or hyperstrophic, not sinistral. In other words, the normal spire has sunk inward, as it were, and may even be coiled in such a way as to produce an umbilicus. The normal base may be flat or protrude to resemble a spire in every respect. Hence a shell is produced that appears to be sinistral although it is actually dextral. The "spire" of such a shell is homologous with the base of what may be called a normal dextral shell and its "base" is homologous with the spire. (See fig. 2.)

Hyperstrophy is exceedingly rare among living gastropods, occurring most frequently as a specialization only in the embryonic nucleus of some opisthobranch gastropods and in the adult stage of a few end members of various highly specialized groups such as pteropods, Ampullariidae, and pulmonates. If it were to occur in adults of species with unknown soft parts it would be difficult to distinguish from sinistrality except on collateral evidence. One line of collateral evidence is that supplied by the peculiar angulation on the "base" of these early Paleozoic shells. If we regard these shells as hyperstrophic, the angulation is no longer anomalous. It becomes the trace of the dorsal anal emargination. There is another line of collateral evidence that is exceedingly pertinent to at least one of the Paleozoic genera that is included in the group we are discussing and it seems very strong evidence indeed. This evidence is furnished by the operculum which is preserved in this genus because it is calcified.

The gastropod operculum is basically corneous (conchyolin) but in some groups the corneous operculum is partially or wholly calcified and in some forms this makes the operculum very massive. Only where it is calcified is the operculum of fossil forms preserved. The embryonic operculum is a minute disk that grows by incremental additions to a margin or margins. Where the increments are added markedly to one side of the margin as against the other sides, growth may be in a spiral and such a spiral operculum, as seen on the external face of the operculum in dextral gastropods, always grows from the nucleus in a counterclockwise direction. In sinistral gastropods it is clockwise. Now, in one of the genera of Paleozoic gastropods of the group we are considering, the operculum was thick and calcified, consequently it is not only frequently preserved but in some specimens it has been found in place in the aperture. The genus is *Maclurites* LeSueur, 1818 (pl. 2, fig. 12). In *Maclurites* the operculum is in the form of an open spiral and the direction of coiling, as seen on its outer face, is counterclockwise. Hence, as pointed out by S. P. Woodward as early as 1854 (p. 202), the shell of *Maclurites* is not sinistral, as has often been supposed, but dextral and hyperstrophic. We do not know the operculum in any other of the genera included in the group under consideration. Nevertheless, as I have endeavored to show, the group we are considering appears to be a natural unit and we may therefore with reasonable assurance attribute to the other genera the character of hyperstrophy that the angulation on the "base" of the whorls suggests and that the operculum of *Maclurites* seems to confirm.

Assuming that we have solved the problem of the coiling in the group under consideration, namely that it is hyperstrophic dextral rather than sinistral, we are faced in consequence with an even more difficult problem. What is the meaning in terms of soft anatomy and of phylogeny of a rather large group of dextral hyperstropic forms introduced so very early in the history of the Gastropoda? Since this group seemingly became extinct before the close of Devonian time, it left no recognized descendants among living gastropods that might throw some light on its organization. As suggested above, hyperstrophy is very rare among living gastropods and occurs only as a secondary acquisition in groups far removed from any possible connection with our early Paleozoic group. We can only surmise what the anatomy of the soft parts of the Paleozoic forms might have been. The shells are coiled and coiled asymmetrically. These facts suggest torsion and possible asymmetry in the primitively paired organs. But, as the shells are hyperstrophic and appear in the fossil record shortly before the first known pleurotomarians, the asymmetry possibly may be very different from that of the main line of gastropod descent. Figure 9 shows hypothetical restorations of the hyperstrophic genus *Palliseria* (pl. 2, fig. 11) a close relative of *Maclurites* (pl. 2, fig. 12). Accepting the notch keel surrounding the umbilicus as the locus of the anus we find very little room for a right ctenidium and tentatively assume that this and its associated organs had been lost. The operculum of *Maclurites* is not only that of a dextral shell but it shows a startling resemblance to that of the recent *Nerita* in that there are points of attachment for a pair of retractor muscles. A single pair of retractor muscles is a primitive feature shared with the bellerophonts, the more primitive pleurotomarians and the neritaceans. The line of speculation that seems most plausible to me is that this group branched off from the early bellerophonts at some such stage as is represented by *Strepsodiscus* (pl. 1, fig. 8), a bellerophont that commonly shows some asymmetry in a sinistral or hyperstrophic sense. This would accord with chronogenesis, for *Strepsodiscus* precedes in the fossil record *Scaevogyra* (pl. 2, fig. 7), the earliest hyperstrophic gastropod, and both precede the earliest pleurotomarian. If this is true the somewhat angular "base" of *Scaevogyra's* whorl is homologous with the angular dorsum of *Strepsodiscus*. It is further supposed that asymmetry arose in the group under consideration as an early genetic response to the mechanical difficulties of isostrophic coiling as in the main line of gastropod descent that began with the pleurotomarians, but independently and probably in a somewhat different way, and that this, in turn, resulted in the asymmetrical, hyperstrophic shell.

PELAGIELLA AND ITS ALLIES

Doubts have been expressed that the members of this group are actually gastropods in spite of the very close resemblance of their shells to those of gastropods. Thus Wenz wrote in 1938 (p. 95) of *Pelagiella:* "Systematische Stellung Fraglich; vermutlich uberhaupt nicht zu den Gastropoden gehörig." The late Dr. E. O. Ulrich is said to have held the opinion that they were "pteropods," that is to say, allied to the hyolithids.[13] The hyolithids are no longer regarded as true pteropods or even as gastropods for that matter. The true pteropods are highly specialized opisthobranch gastropods of Tertiary

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[13] Oral communication from Dr. Josiah Bridge.

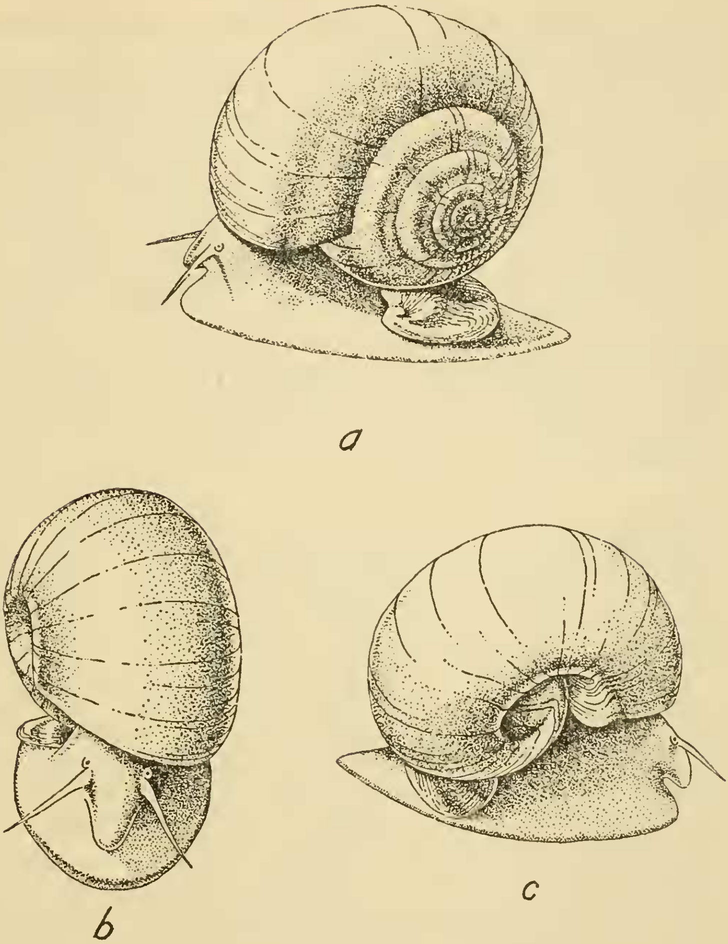

FIGURE 9

Three views of a restoration of *Palleseria longwelli* (Kirk), about × $\frac{3}{4}$.

a, View of the left side. Note the direction of coiling and the protruding, spirelike base.

b, Anterior view.

c, View of the right side. Note here and on the anterior view (*b*) the umbilicus occupying the side where a spire would be in a dextral orthostrophic gastropod. Note especially that the ridge surrounding the umbilcus is the locus of a notch. This notch, an anomalous feature if the shell is regarded as sinistral, is believed to be the anal emargination. If this is correct there is very little space for the primitive right ctenidium and probably it has been lost.

and Recent times, in many respects the farthest removed from the primitive stock of any of the class.

Matthew, in erecting the genus in 1895, seemed to regard *Pelagiella* as a heteropod. The heteropods are again a highly specialized group of late Cretaceous to Recent times, although being prosobranch, not quite so far removed morphologically from the primitive stock as the opisthobranch pteropods. These quite unacceptable assignments serve to accentuate the difficulties in finding a place for these forms in the Gastropoda. My own difficulties derive from the fact that if *Pelagiella* and its allies are gastropods, the hypotheses I have been setting up cannot include them, except peripherally. Otherwise these hypotheses must be abandoned or extensively modified in such ways that they would meet with greater difficulties in other directions than the difficulty presented in removing this obviously questionable group to a peripheral position or eliminating it from the Gastropoda altogether.

Pelagiella and its allies occur in company with the first recorded monoplacophoran gastropods in the rocks of early Cambrian time and are not only coiled but asymmetrically coiled. Thus, if they are gastropods, they appear superficially to have advanced well beyond the isopleuran monoplacophoran stage, the anisopleuran isostrophic stage, and even beyond the pleurotomarian stage of the main line of gastropod evolution. Therefore, since they are contemporaneous with the earliest known monoplacophorans, and the earliest and most primitive known representatives of one of the two hypothetically more primitive stages and precede the others by a considerable interval of geological time, the difficulties are obvious.

I do not wish to consume space in laboring the problem at too great length for, with our present lack of knowledge of their anatomy and even of their conchology, it is not soluble. I am not prepared to abandon the hypotheses as to the derivation of the main lines of gastropod descent until other hypotheses are presented that better explain the observed facts. Although it is recognized that the fossil record is imperfect, I am not prepared to assume that it is so very faulty that its bearing on the broader aspects of chronogenesis is to be set aside. There are various other possibilities that might be called upon to account for *Pelagiella* and its allies as gastropods. For example, can it be that they represent a branch from the monoplacophoran stock that acquired torsion and asymmetry independently in pre-Cambrian time, perhaps bypassing an isostrophic stage? There is little evidence one way or another but I think it extremely unlikely. Or can it be that they are monoplacophorans that carried their tendency to coil anteriorly to such a point that the resulting inconvenience of a coil poised above the head gave survival value to any mutation that set the coil asymmetrically to one side, as it were? This again appears to be extremely unlikely. It would require a symmetrically coiled predecessor and no such form is known.

Finally then, I share the doubts of my predecessors, expressed or implied, that *Pelagiella* and its allies are gastropods, but I shall go further than they have gone in that I shall not attempt to force them into a phylogenetic classification of the gastropods that appears to have no place for them. I shall very tentatively assign them the peripheral position of a shoot from the same pre-Cambrian root as the main trunk of the gastropod family tree originating obscurely in pre-Cambrian and of otherwise little-understood affinities. It would be helpful if I could assign them elsewhere in the animal kingdom, but I cannot do so.

Before leaving the subject of *Pelagiella* and its allies it may be well to review briefly and in general terms their chief characteristics. The shells are coiled and of from one-half to about three whorls. The coil is always asymmetrical. For the most part they are small and many are minute, a millimeter or two in diameter. The apical end of the whorl, the nucleus, appears in some to be laterally flattened and somewhat blunt, reminding one of the tip of a ram's horn, and in some forms slightly swollen. The whorls are ovoid in section, the narrow end of the ovoid being at the periphery. The spire is always low, varying in that respect from depressed to umboniform. In the forms with a depressed spire the base is arched; in those with an arched spire it is flattish. The shells of any one species appear to be rather variable and it is probable that both dextral and sinistral forms occur in some species. The ornamentation consists of fine, faint lines of growth and, on some forms, a single faint revolving lira, seemingly both above and below the periphery. The growth lines are somewhat drawn back at the rounded periphery, thus suggesting a broad, peripheral sinus. No operculum is known and there is no information on muscle scars. In some specimens of *Pelagiella,* Matthews reports and figures a groovelike constriction in the shell (or its steinkern?) close to the apertural margin. It is not present on Matthew's primary types of *Pelagiella atlantoides* (Matthew), the genotype (Knight, 1941, p. 237), but does occur on rare specimens subsequently assigned to the species by Matthew. It may be a mark of maturity or old age. Possibly the constriction is seen only on the steinkern in which case it might mean only that the apertural margin was thickened within and the thickening is invisible on the outer surface of the shell.

This group, in which I include Cambrian species mistakenly referred by authors to such genera as *Straparollina* Billings, *Straparolus* Montfort, *Euomphalus* Sowerby, *Raphistoma* Hall, *Ophileta* Vanuxem, and *Platyceras* Conrad, is in urgent need of intensive study, as are all Cambrian gastropods and gastropodlike forms for that matter. Several names have been proposed for supposed genera, mostly on the basis of quite inadequate studies. Besides *Pelagiella* Matthew, 1895, there are *Parapelagiella* Kobayashi, 1939 (p. 287), *Protoscaevogyra* Kobayashi, 1939 (p. 286), and *Proeccyliopterus* Kobayashi, 1939 (p. 286). The last three seem to be erected on characters of very doubtful value or are differentiated from *Pelagiella* on mistaken concepts of the characters of *Pelagiella* itself.[14] Still another genus, *Semicircularea* Lochman, in Lochman and Duncan, 1944 (p. 44), was erected for the forms with only about one-half whorl often misidentified as *Platyceras* by previous authors. *Pelagiella* and its allies range throughout Cambrian and perhaps into early Ordovician time.

TAXONOMIC CONCLUSIONS

As a result of our findings on our descent of the family tree and of the paleontological and neontological considerations given above, we have arrived at tentative hypotheses that force on our attention certain taxonomic conclusions. The first is that, since the monoplacophoran gastropods seemingly share with the polyplacophorans the basic isopleuran plan of organization, the two should be brought more closely together than has been customary in most classifications. The second is that, since the Anisopleura as the result of mutation arose suddenly from a monoplacophoran ancestor, and since certain anatomical features of both are very similar, the relationship between them is too close to permit them to be arranged in separate classes comparable in degree of differentiation to the other molluscan classes. The third is that, although the isopleurans and the anisopleurans should be placed in a single class, the gulf between them, both anatomically and in time, is profound and that, therefore, it seems appropriate to rank each as a subclass. On the basis of these three considerations we present the following revised definitions of the class

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[14] It is unfortunate that the belief that the supposed characters of two of them suggested that they were ancestral to later genera of quite different affinities and led to the fixation of those ideas in the names given them. The proposal of names embodying phylogenetic concepts is most unwise.

Gastropoda and its major subdivisions, the subclasses Isopleura and Anisopleura. There are also other conclusions as to the subdivisions of the next lower rank but consideration of these is postponed until the class and the two proposed subclasses are dealt with.

Class GASTROPODA Cuvier

So great is the range of special morphological modifications in the class that it is exceedingly difficult, if not impossible, to draw up a brief diagnosis that will cover all gastropods without excluding some forms that clearly must be included. The return of the isopleurans to the class, however necessary it appears, increases the difficulties, for we thereby reduce the convenient criteria of torsion and of a single shell to a status diagnostic of subdivisions of lower rank.

The gastropods may be defined as mollusks with a differentiated head, a flat creeping foot, and a single basically conical shell. In a few gastropods specialized for free swimming the foot may be modified into finlike organs, in the polyplacophorans the primitive single shell has been divided transversely into eight segments, and in some highly specialized forms the shell has disappeared in the adult. In many others the cone is attenuated and coiled. Primitively marine, they have become adapted also to fresh waters and to terrestrial life. They are found at nearly all latitudes and nearly all altitudes from the depths of the oceans to high mountains. They appear in the fossil record in Lower Cambrian rocks and are flourishing today.

Subclass ISOPLEURA Lankester.—Gastropods that retain throughout life both in the shell and in the soft anatomy the primitive bilateral symmetry of the class. They are entirely marine and always rare. They first appear in the fossil record in Lower Cambrian rocks and carry through to the present. They probably originated in pre-Cambrian time.

Subclass ANISOPLEURA Lankester.—Gastropods that undergo torsion during the veliger stage. The Anisopleura are often abundant and are tremendously diversified in morphology and in habitat. They first appear in the fossil record as primitive forms in Lower Cambrian rocks and are flourishing today.

MAJOR DIVISIONS OF THE SUBCLASS ISOPLEURA

Order POLYPLACOPHORA.—Isopleuran gastropods with the shell made up of eight plates arranged along the midline of the dorsum; head not provided with eyes; shell eyes, or aesthetes, may be present. Polyplacophora range from late Cambrian time to the present, are always marine and relatively rare.

The subdivisions of the Polyplacophora will not be considered here.

Order Monoplacophora.—Isopleuran gastropods with a single conical shell with the apex subcentral or pointed forward; some possibly with aesthetes. Marine, Lower Cambrian–Devonian.

Before considering the subdivisions of the Monoplacophora it may be well to repeat that I do not consider *Discinella* Hall, 1871, *Mobergella* Hedström, 1923, or *Barella* Hedström, 1930, to be monoplacophoran gastropods but hyolithoid opercula. *Conchopeltis* Walcott, 1879, I regard as probably a scyphozoan and certainly no mollusk. *Chuaria* Walcott, 1899, is entirely problematical. (Knight, 1941, p. 20.)

Family Tryblidiidae Pilsbry, 1899

Subfamily PALAEACMAEINAE Grabau and Shimer, 1909

Relatively low to high, cap-shaped shells with apex subcentral to slightly anterior. Muscle scars (observed only in *Archaeophiala*) discrete and arranged in six (or eight?) symmetrical pairs; ornamentation basically concentric undulations.

Genera

Scenella Billings, 1872 (pl. 1, fig. 1) (=*Parmophorella* Matthew, 1886), Cambrian.

Helcionella Grabau and Shimer, 1909 (pl. 1, fig. 2), throughout the Cambrian.

Palaeacmaea Hall and Whitfield, 1872, Upper Cambrian.

Archaeophiala Koken, in Perner, 1903 (pl. 1, fig. 3) (=*Scaphe* Hedström, 1923, *Scapha* Hedström, 1923, *Patelliscapha* Tomlin, 1929, and *Paterella* Hedström, 1930), Ordovician.

Calloconus Perner, 1903, Lower Devonian.

In the Silurian what appears to be a new genus hitherto unrecognized is represented by *Palaeacmaea? solarium* Lindström, 1884 (p. 59).

Subfamily TRYBLIDIINAE Pilsbry, 1899

Spoon-shaped shells with the apex at or overhanging the anterior end. Muscle scars (observed in *Tryblidium, Pilina, Drahomira, Proplina,* and partially in *Cyrtonella*) essentially similar to those of the foregoing family; ornamentation concentric-lamellar or radiating.

Genera

Tryblidium Lindström, 1880, Silurian.

Cyrtonella Hall, 1879, Devonian.[15]

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[15] I have given my reasons for including *Cyrtonella* Hall in the Tryblidiidae elsewhere (Knight, 1947b, p. 267).

Helcionopsis Ulrich and Scofield, 1897, Ordovician.
Drahomira Perner, 1903, Ordovician.[16]
Vallatotheca Foerste, 1914, Ordovician.
Pilina Koken, 1925, Silurian.
Proplina Ulrich and Bridge in Kobayashi, 1933, Upper Cambrian—Lower Ordovician.[17]

Family HYPSELOCONIDAE, new

Narrowly conical shells with the apex over the narrower (anterior?) end but tilted slightly backward. Ornamentation growth lines or faint radiating undulations; muscle scars unknown.

Genera

Hypseloconus Berkey, 1898, Upper Cambrian–Lower Ordovician.[18]
Pollicina Holzapfel, 1895, Ordovician.

Family ARCHINACELLIDAE, new

Low conical shells with the apex at or overhanging the anterior end. Ornamentation growth lines or radiating lirae; muscle scar a broad, continuous ring, narrowing in front where it passes below the apex. Ordovician.

Genera

Archinacella Ulrich and Scofield, 1897.
?Ptychopeltis Perner, 1903.[19]

It is possible that *Helcionopsis* will find a place here rather than with the Tryblidiidae when its muscle scars are discovered.

Order APLACOPHORA.—In this order there is no shell, and it is consequently unknown as a fossil. I have no comments but retain it here.

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[16] *Drahomira* is a name published, but not adopted, by Perner, 1903 (p. 23, footnote) for *Tryblidium glaseri* Barrande in Perner, 1903 (p. 23), genotype by monotypy. This name was overlooked by me in the preparation of "Paleozoic Gastropod Genotypes" (Knight, 1941). Seemingly it is the valid name for a distinct genus of this family.

[17] The muscle scars of *Proplina cornutaformis* (Walcott), the genotype and only species referred to the genus in published literature, are unknown. However, the material assembled for a monograph on Ozarkian and Canadian gastropods by E. O. Ulrich and Josiah Bridge is available to me and several species referred to the genus show them clearly.

[18] For comments on the supposed multiple paired muscle scars of *Hypseloconus* see Knight, 1941 (p. 158).

[19] Although Perner described a scar for *Ptychopeltis*, examination of his specimens failed to disclose valid evidence for it (Knight, 1941, p. 288).

SUBCLASS ANISOPLEURA LANKESTER

Except for reviving Lankester's subclass Anisopleura, equivalent without the Monoplacophora (Tryblidiacea of Wenz) to the class Gastropoda of Wenz, 1938, I am now proposing few changes. To the Bellerophontacea, which are retained as Prosobranchia, are added the family Coreospiridae with the genera *Coreospira* Saito (pl. 1, fig. 7), *Cycloholcus* Knight, and *Oelandia* Westergård (pl. 1, fig. 5), but not without a residuum of doubt, and the superfamily Macluritacea is erected in the Prosobranchia. The Macluritidae of Wenz form its nucleus and other families composed of related elements are assembled with it. The revised taxonomy of the group will be presented as a part of another paper. The included genera are listed on pages 36-37 of this paper. In all other respects the Anisopleura are left as Wenz had them but because of lack of opportunity for intensive study rather than because of detailed endorsement of his arrangements.

APPENDIX

INTERPRETATION OF THE BELLEROPHONTS

AMPHIGASTROPODA VS. PROSOBRANCHIA

The genus *"Bellerophon"* of the older workers and some neontologists (now expanded to a superfamily, the Bellerophontacea, with four families and something like fifty genera and subgenera) has been difficult to understand and to classify. Its isostrophic habit of coiling is almost unique in the Gastropoda. This and the fact that the entire superfamily has been extinct since Triassic time and affords no living examples from which soft parts can be demonstrated have seemingly left us with little information to go on. The broad morphological pattern of the soft parts must be inferred since it cannot be observed directly.

De Koninck in 1883 (p. 121) reaffirmed on a more rational basis his suggestion of 1843 (p. 337) that the bellerophonts were prosobranch gastropods. Before 1883 the bellerophonts had been regarded as cephalopods, or as heteropod gastropods. Some specialized forms such as *Pterotheca,* originally described as brachiopods or pelecypods, have been regarded as pteropods. Since that time they have been classified as prosobranch with the Docoglossa, or as a separate class of Mollusca, the "Amphigastropoda." I can subscribe to none of these views except perhaps the main thesis of de Koninck in 1883, although not to the details.

As stated previously, Wenz's great contribution to theory in 1938

(p. 59) was the idea that the Tryblidiacea were primitive untorted gastropods. This I applaud and accept. But he also regarded the bellerophonts as untorted gastropods similar to the Tryblidiacea, on the grounds of symmetry and an unsupported assumption that the slit and band are not to be compared with the seemingly homologous feature in the pleurotomarians. On this point I must part company with him. Curiously, if I read the story aright, Wenz seems to be following part way in the footsteps of many of his predecessors, who regarded the bellerophonts as prosobranchs on the grounds of the following chain of reasoning: The early cup-shaped shells are symmetrical and resemble the living patellids; therefore they are to be classified with the latter as Docoglossa and prosobranchs. The bellerophonts are also symmetrical; therefore they are closely related to the patellids and are also Docoglossa and prosobranchs.

But Wenz in recognizing the early cup-shaped mollusks, the Tryblidiacea, as nontorted gastropods changed the first premise of the customary chain of reasoning and the bellerophonts, still linked with these early cup-shaped shells, are, to Wenz, like them nontorted gastropods.

The weakness in both lines of argument is the overvaluing of the symmetry of bellerophonts as a criterion of relationship to the symmetrical cup-shaped shells whether patellids or tryblidians, the undervaluing of the many manifest differences between the bellerophonts and either of the other two, and the undervaluing of several manifest anatomical homologies between the bellerophonts and the asymmetrical but coiled prosobranch pleurotomarians.

Fundamental to the undervaluing of bellerophont-pleurotomarian homologies is a failure on the part of Wenz and some neontologists to recognize that torsion and the development of lateral asymmetry are two distinct processes. Undoubtedly torsion set up unstable conditions that favored the natural selection of mutations, such as lateral asymmetry, that would result in a more efficient organism, but lateral asymmetry is not to be confused with torsion or what I have called torsional asymmetry. Although torsion is a prerequisite for asymmetry, asymmetry does not necessarily follow from it. It is as though this school of thought believes that the muscular pull that initiates torsion also distorts the lateral symmetry. I know no evidence that supports such a view. It is true, of course, that except in the Isopleura all gastropods living today show lateral asymmetry at some ontogenetic stage and the lateral asymmetry is initiated in the veliger larva immediately after torsion. But it does not follow that it was always universally thus. The view that asymmetry was the immediate or concommitant mechanical result of torsion and in consequence became a part of gastropod heritage smacks somewhat of Lamarckianism and in any case cannot be sustained.

Returning to Wenz's views, in 1938 they seem to have been approximately as I have stated them above. On the basis of the lateral symmetry alone he felt that the bellerophonts were closely related to the tryblidians and consequently had not undergone torsion. Although he gave no systematic expression to these views at that time, classifying both the Tryblidiacea and Bellerophontacea as Prosobranchia, it was his opinion that both were probably out of place in that position.

Feeling insecure as to his interpretation of the bellerophonts he was quite rightly searching for corroborative evidence, and he felt that the discovery in the bellerophonts of multiple, paired dorsal muscle scars like those of the tryblidians would be strong supporting evidence, as indeed it would. In 1937 he wrote to me asking what I knew of bellerophont muscle scars and that started the chain of events about which I wrote ten years later (Knight, 1947). Briefly, a specimen of the supposed but somewhat atypical bellerophant *Cyrtonella mitella* (Hall) was discovered which seemed to support fully Wenz's views in that the unmistakable record of two pairs of dorsal muscle scars (not three as Wenz wrote) was clearly visible on that part of the steinkern that was exposed. Possibly other scars may be covered by matrix. Feeling that his views as to the close relationship of the bellerophonts and tryblidians were fully vindicated, Wenz published his paper giving systematic effect to those views by employing for them a subclass, the Amphigastropoda (Wenz, 1940).[20]

An interesting point about tryblidian muscle scars noted in *Tryblidium, Archaeophiala,* and *Cyrtonella* is that each scar has on the side toward the margin of the shell a smaller, fainter scar as though it were the shadow of the scar cast before it. Wenz, who had never seen the specimen of *Cyrtonella mitella* he figured, misinterpreted a pair of these shadow scars, shown in the photograph sent him by Yang, as a principal scar. This is why he mistakenly reported three visible pairs of scars. The physiological significance of the "shadow scars" is

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[20] Actually the Amphigastropoda consisting of only the bellerophonts, was erected as a new class of mollusks by Simroth in 1906 (p. 839), who was followed by Thiele in 1935. Simroth's course, and especially Thiele's, was supported only by the gratuitous assumption that the soft anatomy was without torsion and bilaterally symmetrical. Amazingly, Thiele assumed also "eine änliche schwimmende Lebensweise—wie die Nautiliden" (Thiele, 1935, p. 1125) in which he was followed by Wenz.

obscure but their presence is an additional evidence that *Cyrtonella* is a tryblidian.

Although the paired dorsal muscle scars on the specimen of *Cyrtonella* were discovered in my laboratory and although it was on my suggestion that Yang disclosed the discovery to Wenz, my views as to its significance were quite different from those so promptly published by Wenz in 1940. The more probable interpretation that *Cyrtonella,* a genus that was even then somewhat doubtfully placed in the Bellerophontacea and quite as easily interpreted as a tryblidian, should be placed in the Tryblidacea instead of the Bellerophontacea seems never to have occurred to Wenz.

Fortunately I was able to discover the muscle scars of two unquestionable bellerophont genera a few years later, *Sinuites* (pl. 1, fig. 11) and *Bellerophon* (pl. 1, fig. 13) (Knight, 1947). They consist of a single symmetrical pair. Each muscle was attached to the opposite end of the colummella about one-half whorl within the aperture, a position that would permit them to serve effectively as pedal retractors. They are not dorsal and not multiple pairs. Both of those facts are seemingly fatal to Wenz's arguments as to the closeness of the relationship between the tryblidians and the true bellerophonts.

Wenz displays a number of views to which I must take exception. For example, he accepts the wholly conjectural and long-rejected views of Lang (1891) as to the gradual development of torsion in the gastropods. He treats the bellerophonts and pleurotomarians as being present in early Cambrian rocks. In terms of genera recognized by him, neither appeared until late Cambrian time. Under the influence of his overestimate of the significance of external lateral symmetry in the bellerophonts he fails to even consider the close homologies between bellerophonts and pleurotomarians. Finally, he seems to hold the view first proposed by Deshayes in 1830 (p. 135) and abandoned by most students well before the close of the nineteenth century that the bellerophonts "tended toward a freely swimming, nektonic mode of life" (translation from Wenz, 1938, p. 59). I know of no evidence whatever that would support such a view and would be interested indeed to learn of a molluscan swimming mechanism that would be powerful enough to sustain the massive shells of some bellerophonts above the sea bottoms. It seems highly probable that the bellerophont foot conformed in general to the pattern shown by other Archaeogastropoda. It was adapted to creeping, not to swimming.

I regard the bellerophonts as prosobranch Archaeogastropoda close to and probably ancestral to the pleurotomarians which they precede in the fossil record. The bellerophonts share with the pleurotomarians (1) a shell that typically has deeply hollow, usually closely coiled whorls, (2) a sinus or slit which, if a slit, generates a slit band, (3) a single pair of lateral retractor muscles,[21] and (4) seemingly a single pair of each, of ctenidia, auricles, etc. They differ principally in that the coil of the bellerophont shell is bilaterally symmetrical (isostrophic) and that of the pleurotomarian shell is an asymmetrical orthostrophic helicoid, in my view a difference of little significance for classification but of profound import for understanding gastropod evolution.

Comparing the bellerophonts with the tryblidians we find they have one feature, and only one, in common: externally the shell of each is bilaterally symmetrical. But in respect to the first three categories in the foregoing paragraph, the tryblidians have (with a very few exceptionally high conical shells) (1) a shallow cup- or spoon-shaped shell with the apex bent toward one end, but no coiling, (2) no sinus or slit, and (3) multiple (usually six or eight) symmetrical pairs of dorsal muscle scars.

Let us look for a moment at these points of agreement and disagreement. The agreement between the bellerophonts and pleurotomarians on points 1 and 3 can only mean that we have a shell with a deep body cavity into which the head and foot can be withdrawn by the retractor muscles which are properly placed in both for the operation. Point 2, the sinus or slit can only be an anal emargination, a feature that is known otherwise only in prosobranchs and especially in the Archaeogastropoda, and which is accepted by many neontologists such as Garstang, Yonge, Crofts, and many others as an adaptation for sanitation after torsion had created a need for it. The bilateral symmetry of the shell can no more be considered a character of subclass or even ordinal rank than that same symmetry can be employed to link two groups so different on other points as the bellerophonts and tryblidians.

Need we continue to point further fundamental differences between the pleurotomarians and bellerophonts on one hand and the tryblidians on the other, differences such as the impossibility of at least the low, cuplike tryblidians pulling their head and foot into the shell? In that respect they probably resembled the chitons and the secondarily symmetrical fissurellids and patellaceans. Since the muscle

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[21] The living pleurotomariid genera or subgenera *Perotrochus* Fischer, *Entemnotrochus* Fischer (pl. 2, fig. 4), and *Mikadotrochus* Lindholm, "*Pleurotomaria*" of authors, have only a single retractor muscle, although other living pleurotomarian genera have a pair.

scars of the high and narrow species of *Helcionella* (pl. 1, fig. 4) in the tryblidians have never been observed, it is more difficult to speculate profitably as to whether the muscles are so placed that they could or could not have withdrawn the head and foot into the shell. It is possible that they could, especially if, as I am suggesting, the reduction of the pedal muscles from eight pairs to one pair may have occurred first in them. Need it be pointed out to those who regard the anal emargination in the bellerophonts as posterior that no known or reasonably imaginable nontorted mollusk has or needs a slit or sinus to provide egress for the contaminated water of a posterior anus? Certainly the chitons and the tryblidians do not. Again, have those who infer that bellerophonts are primitively orthoneurous nontorted "Amphigastropoda" ever tried to imagine the animal with its large, heavy coil anterior and overhanging the head? The shell in many bellerophont species is not only thick and heavy but may carry a massive parietal callus as well. To me such an arrangement appears highly improbable, bordering indeed on the fantastic. It is suggested that the reader turn to figure 7, *a,* on page 30, where a restoration of a small very primitive bellerophont, with no parietal callus, is presented as though it were primitively orthoneurous and exogastric, may help him to visualize it.

In summary, it appears to me that the evidence for the view that the bellerophonts were prosobranchs, is very strong and the evidence that they were primitively orthoneurous "Amphigastropoda" very weak indeed.

Soft anatomy of the bellerophonts.—We now know enough of bellerophont shell morphology and enough of the morphology of living examples of the obviously related pleurotomarians that we may speculate with considerable safety on the general nature of bellerophont soft anatomy and perhaps even on its physiology and habits.

One may be quite confident that they were aspidobranchs with a high degree of bilateral symmetry reflected in symmetrically paired ctenidia, osphradia, hypobranchial glands, auricles, kidneys, and perhaps even gonads. They probably crawled on the sea bottom on a generalized gastropod foot. It seems probable that like other aspidobranchs they fed chiefly on vegetable matter and were rhipidoglossate. Nothing is known of the bellerophont operculum, if there was one.

Perhaps a diagrammatic restoration of some of the more significant soft parts with an interpretation of the course of the water currents in the mantle cavity will save pages of words.

On figure 10 is shown a shell of a bellerophont species, *Knightites multicornutus* Moore, 1941 (p. 153), with the soft parts restored in

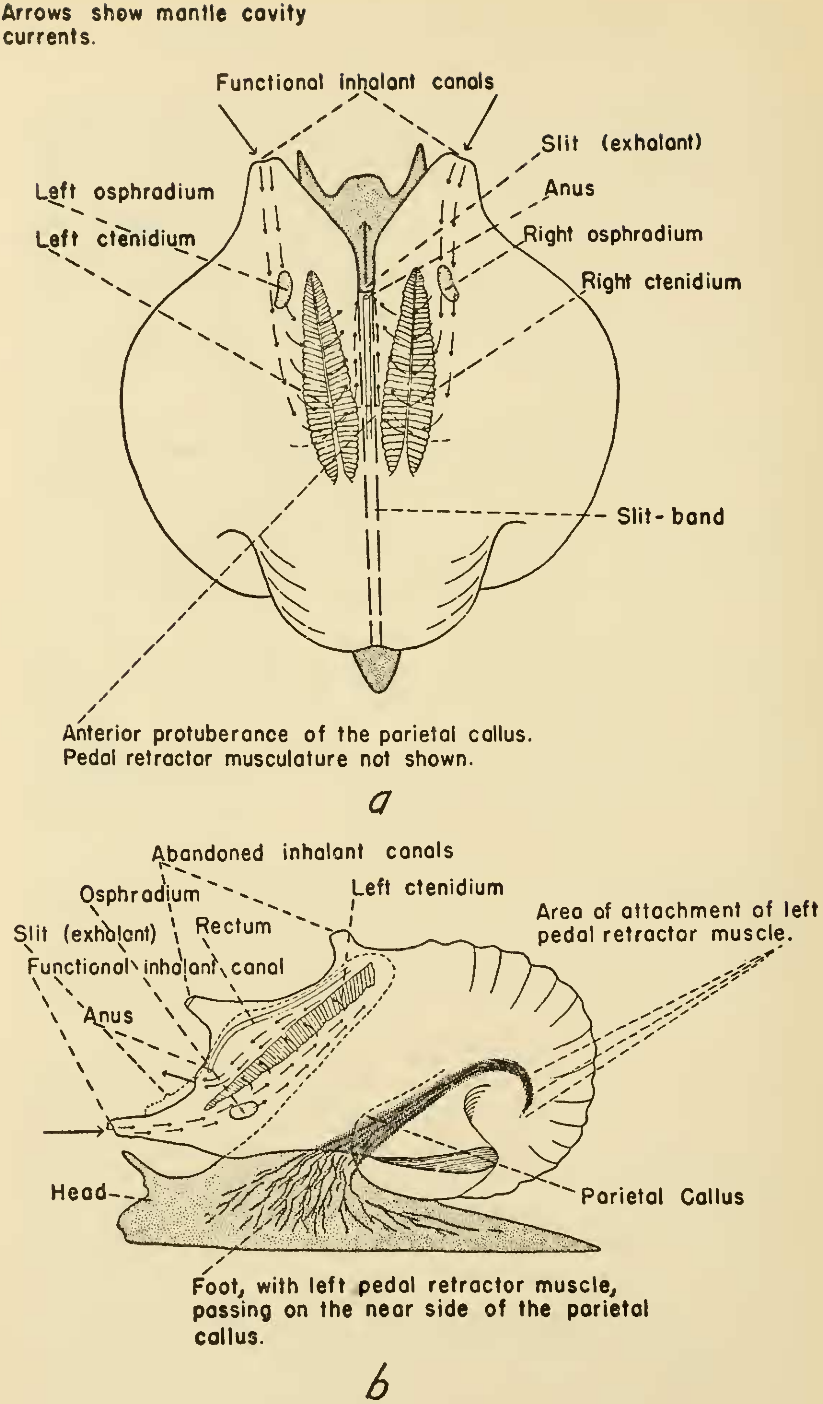

FIGURE 10

(See opposite page for explanation.)

terms of the above interpretation. It is a modification of figure 7d in Moore, 1941 (p. 158). I have abandoned the ideas expressed in figures 7a-c as untenable in the light of more accurate knowledge of the aerating currents in *Haliotis* than I then had. The extended periodic, paired canals on each side of the slit and slitband in *K. multicornutus* interested me very much. It occurred to me that they gave a clue to the region on the mantle lip through which passed the currents of water that aerated and flushed out the mantle cavity. The works of Yonge and Crofts on the aerating currents in various gastropods including the pleurotomarian *Haliotis* seem to reinforce the suggestion made by the canals of *K. multicornutus,* so that one can infer the probable course of the principal water currents in that species and probably in all generalized bellerophonts. This inferred circulation is in all respects that of a prosobranch and seems a reasonable approximation to the probable condition during life.

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Figure 10

Two views of a diagrammatic restoration of *Knightites multicornutus* Moore (Bellerophontacea, Bellerophontidae), approximately × 2. The shell is drawn as though it were partly transparent so as to show some of the fleshy organs. The arrows show the probable path of the principal aerating and cleansing currents. Although most bellerophonts did not have inhalant canals as did *Knightites* it is thought that the path of the currents and regions of their entrance and exit were approximately the same as inferred for *Knightites.* In living *Haliotis* where the details are known the paths are homologous in every respect.

a, Dorsal view.

b, Left side view. The fibers of the left retractor muscle are shown in a highly schematic fashion as though they anastomose into the muscles of the foot (which are not shown).

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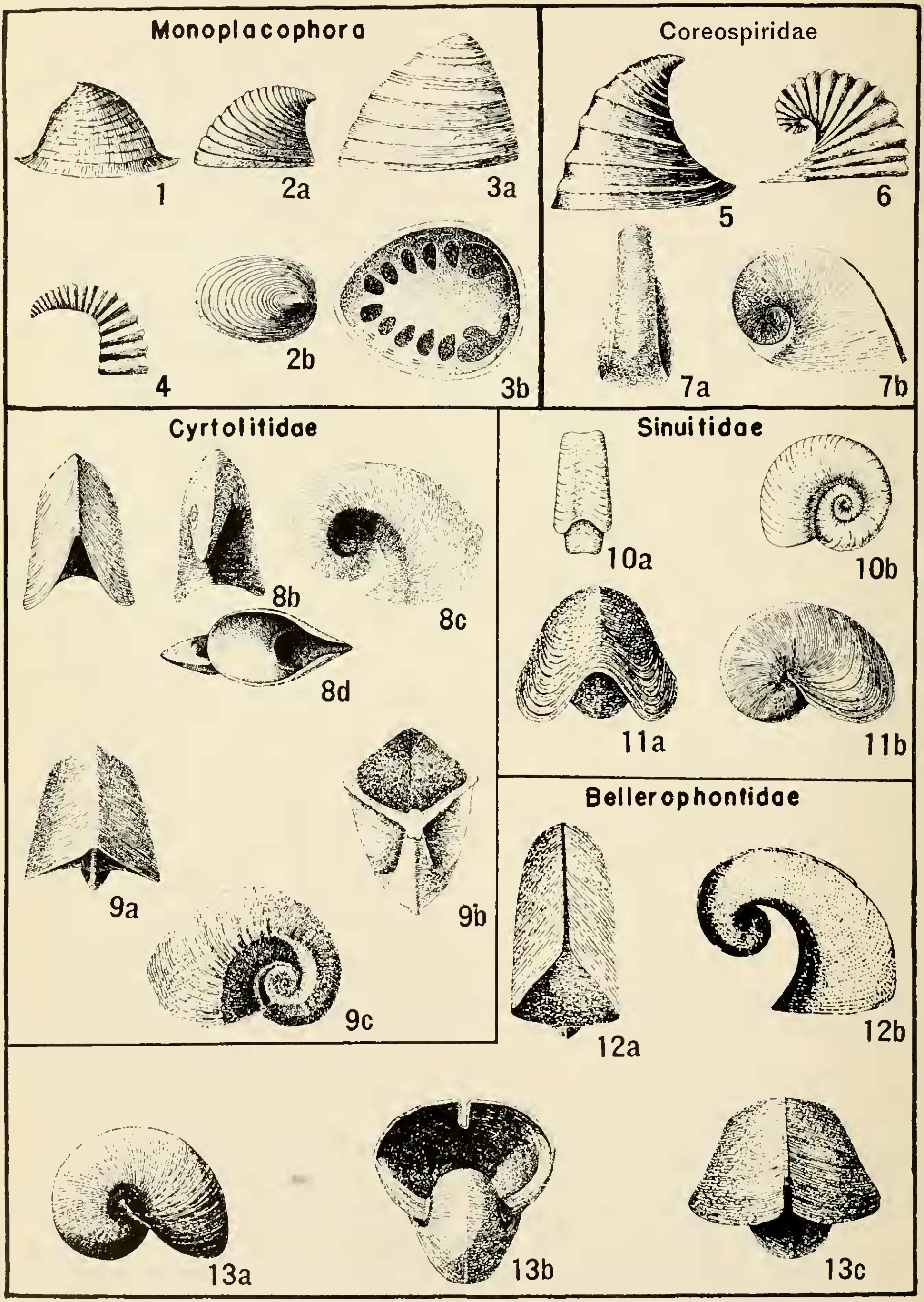
Just as this work reached page-proof stage, a copy of the "Traité de Paléontologie," published under the direction of Prof. Jean Piveteau, reached Washington (Traité de Paléontologie, vol. 2, 1952). The chapter on the Gastropoda is by Dr. Geneviève Termier (née Delpey) and Prof. Henri Termier of Algiers. Since I have discussed Mme. Termier's views on gastropods elsewhere (Geol. Mag., vol. 83, pp. 280-284, 1946), I shall say nothing further here except to reaffirm my almost complete disagreement.—J. B. K.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Coreospiridae
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6
7a
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Cyrtolitidae
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8c
8d
9a
9b
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Sinuitidae
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11a
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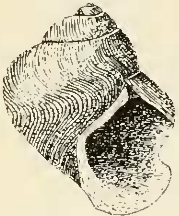
Bellerophontidae
12a
12b
13a
13b
13c

Pleurotomariacea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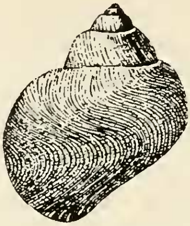
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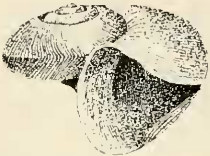
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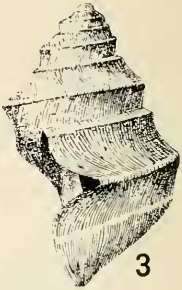
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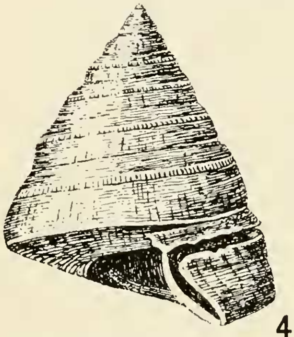
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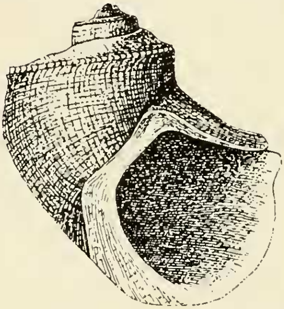
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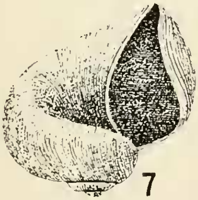
Macluritacea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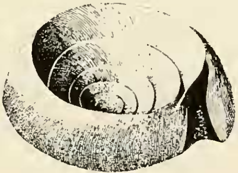
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9a


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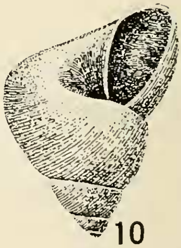
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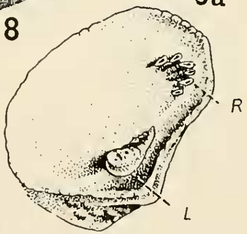

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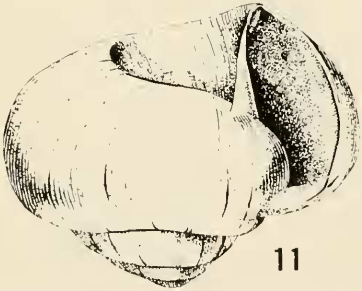
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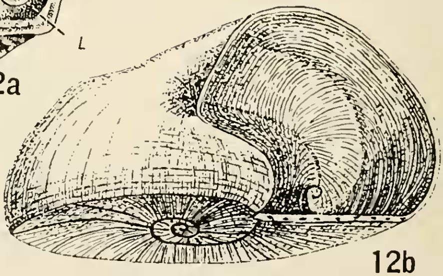
12b

PLATE 2

1-6. Pleurotomariacea.

1a-b. *Sinuopea sweeti* (Whitfield). Upper Cambrian (Jordan member, Trempealeauan), Wisconsin. a, Apertural view. b, Dorsal view. Note the U-shaped anal emargination and compare it with that of *Sinuites cancellatus* (pl. 1, fig. 11a). Approx. × 1. 2. *Schizopea typica* (Ulrich and Bridge). Lower Ordovician (Van Buren), Missouri. Note the deep V-shaped sinus. Approx. × 1. 3. *Loxoplocus (Lophospira) milleri* (Miller). Middle Ordovician (Trenton), New York. Note deep V-shaped sinus generating a band. Approx. × 1½. 4. *Entemnotrochus adansoniana* (Crosse and Fischer). Living, Caribbean Sea. This is one of the species miscalled "Pleurotomaria" by neontologists. Note the deep slit. Approx. × ¼. 5. *Phanerotrema labrosum* (Lindström) not Hall. Lower Silurian, Gotland. The slit, which generates a band, is short. Approx. × 1. 6. *Goniasma* sp. Pennsylvanian, Texas. Note the V-shaped sinus and the very short slit. This is an example of the Murchisoniidae. Approx. × 1½.

7-12. Macluritacea. All these are dextral and hyperstrophic. Hence the orientation, actually the same as for other dextral forms, appears to be up-side down. 7. *Scaevogyra swezeyi* Whitfield. Upper Cambrian (St. Lawrence Member, Trempealeauan). Note the sharp, V-shaped sinus culminating at the circumbilical carina. The sinus is the anal emargination without a reasonable doubt. It should be noted here that the thin shell with expanded aperture in Whitefield's restoration is an error. Wenz (1938, p. 239) grossly exaggerates the error. Approx. × 1. 8. *Lecanospira compacta* (Salter). Lower Ordovician (Roubidouxian), Quebec. Note the deep, V-shaped anal emargination and the circumbilical carina. Approx. × 1. 9a-b. *Onychochilus reticulatum* Lindström. Lower Silurian, Gotland. (After Lindström). a, A longitudinal section. b, Apertural view. Note that the anal emargination is obscure and that circumbilical ridge is rounded and troughlike. Approx. × 2. 10. *Matherella saratogensis* (Miller). Upper Cambrian (Little Falls, Trempealeauan), New York. As in *Onychochilus* the anal emargination is obscure and the circumbilical ridge rounded and troughlike. Approx. × 4. 11. *Palliseria longwelli* (Kirk). Middle Ordovician (Chazyan), Nevada. The anal emargination is angular and culminates at the angular circumbilical ridge. Approx. × ⅔. (See also text figure 9, p. 41.) 12a-b. *Maclurites logani* Salter. Middle Ordovician (Black River), Ontario. a, The operculum, inner surface. Note the attachment rugosities of the left (L) and right (R) retractor muscles. As in *Nerita* the attachment rugosity of the left muscle is an extended projection. b, The shell with the operculum in place, apertural view. The umbilicus is narrower and the circumbilical ridge more rounded than in some species. Note the counterclockwise spiral of the operculum, a feature diagnostic of a dextral gastropod. Approx. × ⅔.